THE ROLE OF CHEMICAL CUES IN THE PREDATORY AND ANTI-PREDATORY BEHAVIOUR OF JUMPING SPIDERS (ARANEAE, SALTICIDAE)

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CONTENTS

ABSTRACT

The role of chemical cues in prey-capture behaviour is studied in jumping spiders (Salticidae). Prior to this study, little attention has been given to how chemical cues influence the predatory behaviour of these spiders with complex eyes and visual acuity unrivalled in any other animals of comparable size. Three categories of predation are considered: salticids preying on conspecifics (cannibalism), salticids preying on non-conspecific spiders (araneophagy) and salticids preying on ants (myrmecophagy). Primary study animals are Portia spp. and Habrocestum pulex. Portia spp. and Habrocestum pulex are known to prefer spiders and ants, respectively, as prey, and each uses specialised prey-capture behaviour against its prefered prey. Here the predatory behaviour of these salticids is shown to be influenced in a variety of ways by chemical cues from prey. A general conclusion is suggested: that reliance on chemical cues is especially pronounced in predators that specialise on particularly dangerous prey.

In Queensland, Portia fimbriata preys on other genera of salticids, with Jacksonoides queenslandicus being the dominant salticid prey species taken. Besides actively stalking J. queenslandicus in the open, P. fimbriata also launches attacks from webs and details of how P. fimbriata uses its web against J. queenslandicus are investigated. Contact and olfactory chemical cues from J. queenslandicus are shown to have three distinct effects on the predatory behaviour of Queensland Portia fimbriata: (1) attracting P. fimbriata to, or inducing P. fimbriata to remain in, areas where there are cues from J. queenslandicus; (2) changing P. fimbriata's behaviour in ways that facilitate prey capture; (3) heightening P. fimbriata's attention to optical cues from J. queenslandicus. No evidence was found that any other prey species has comparable influences on P. fimbriata.

Undirected leaping (erratic leaping with no target being evident) is one of the Queensland P. fimbriata's responses to chemical cues from J. queenslandicus. That this behaviour functions as hunting by speculation is investigated. Experiments show that undirected leaping induces J. queenslandicus to move and thereby reveal its location to P. fimbriata.

Intraspecific conflict in Sri Lankan Portia labiata is particularly violent, often ending in cannibalism. Using size matched conspecifics, two types of testing show that females of this species and population of Portia discriminate between conspecifics on the basis of fighting ability. Other Portia, and other salticid genera, were tested as well, but none of these are as prone to violent aggression and cannibalism. There was no evidence for recognition of fighting ability in any salticid other than Sri Lankan P. labiata.

Habrocestum pulex is shown to rely on chemical cues from ants. Chemical cues from ants induce H. pulex to: (1) remain on soil which has previously housed ants; (2) enter an experimental arm of a Y-shaped olfactometer more often if it contains air from a cage with ants, or if it contains 6-methyl-5-hepten-2-one (an ant alarm pheromone); (3) change behaviour in ways that facilitate ant capture; (4) enhance attention to optical cues from ants.

CHAPTER 1:

INTRODUCTION

When animals evolve specialisation for particular tasks this may be at the cost of limiting their proficiency at performing other tasks. This is the hypothesis of adaptive tradeoffs, an idea that has had a predominant place in much of the ecological, ethological and evolutionary literature (e.g., Levins, 1968, Dukas & Real, 1993), although it has not always been stated explicitly. Sometimes its status has perhaps appeared to be more like an assumption than a hypothesis.

Morphology may provide the most clear cut examples of adaptive tradeoffs. To take an example from spiders, Myrmarachne plateoides O.P. Cambridge is a salticid spider with pronounced sexual dimorphism. The males of this species have exceptionally long fangs, presumably a consequence of sexual selection for display ornamentation (Pollard, 1994). The usual function of fangs, however, is for injecting venom into prey. Myrmarachne plateoides females have fangs which are much shorter than those of males, and females have functional fangs. That is, the female has complete ducts connecting the tip of the fangs to the venom glands in the female's body. However, the male's fangs are ductless. It appears that, as a consequence of sexual selection, the male's fangs have become too long and thin for functional ducts to be feasible. Complete ducts, even if present, would be unlikely to function because of the mechanical problems associated with forcing venom through a long slender tube. It appears that, in evolution, the male has traded off prey capture efficiency when fangs became specialised to function in display.

Unlike morphology, the degree to which adaptive tradeoffs might apply to behaviour is not so clear. Both behaviour and morphology are part of an animal's phenotype, but there are

important differences related to the time frames over which changes are possible for each. An animal's morphology as more or less fixed for extended periods. In contrast there is greater potential for rapid switching in behaviour. For example, birds may rapidly change feeding strategies depending on prey types encountered but do not grow alternative beak types each time a different food type is encountered.

Predatory versatility, which is known for a wide range of animals (Curio, 1976), appears to illustrate how behaviour differs from morphology. The versatile predator has a conditional behavioural strategy, consisting of a repertoire of different tactics specialised for particular prey. The potential for repertoires of predatory morphology appear to be vastly more limited because of the time frame required for most morphological transformations, suggesting that the idea of adaptive tradeoffs may not apply in the same way, or to the same degree, to behaviour and morphology.

There is an alternative way to envisage limitations on behaviour repertoire size. Adaptive tradeoffs in the evolution of behaviour might derive from cognitive limitations. That is, a versatile predator must have a nervous system that can sort and organise the use of the various tactics in its repertoire, and we can expect limits on what nervous systems can do. Cognitive ability might be limited by the size of an animal's nervous system (Staddon, 1983; Dukas & Ellner 1993; Wehner, 1997). Perhaps versatile predators with smaller nervous systems are constrained to have repertoires of tactics which are smaller than the repertoires possible for predators with much larger nervous systems.

It is widely accepted that there is a distinction between the cognitive abilities of vertebrates and invertebrates. Vertebrates tend to be large animals, whereas most invertebrates are considerably smaller. As nerve cells cannot be shrunk indefinitely, smaller animals must suffer limitations in how many neurones are available for the control of behaviour. Cephalopod

molluscs are invertebrates with especially large brains, and it is in the octopus and its relatives that we expect to find invertebrates with especially complex, flexible behaviour. Arthropods, on the other hand, tend to have brains that are orders of magnitude smaller than the brains of better known vertebrates, including all mammals, and it might be in the arthropods that we would expect to find especially clear evidence of adaptive tradeoffs in the evolution of behaviour.

Recent studies suggest that the limitations set by brain size might have been overestimated in arthropods. Perhaps the most challenging examples come from araneophagic (i.e, spider-eating) spiders in the salticid genus Portia. The species in this genus have complex, flexible predatory strategies used for catching and feeding on a wide array of different types of prey including web-building spiders, spiders that do not build webs, spider eggs, and insects. Web-building spiders are not simply stalked or chased down. Instead, aggressive-mimicry signals are made to deceive and manipulate the behaviour of the victim. Different aggressive mimicry tactics are used against different kinds of web-building spiders, and Portia takes on a very wide range of web-building species. It is far from clear how Portia's predatory strategy is simpler or more limited than that of an average predatory vertebrate.

Local adaptation to prey appears to be common in Portia, and repertoire size evidently varies among species and even among populations of single species of Portia. Yet there is no dramatic evidence that adding on additional tactics has been detrimental to the ability of any species or populations of Portia to use the tactics it already has in its repertoire (Jackson & Hallas, 1986a; Jackson 1992a).

In this thesis, I examine another area in which we might expect evidence of adaptive tradeoffs, sensory specialisation. Sensory and behavioural specialisation are different but related topics. An animal's size, especially the size of its nervous system, might be expected to

constrain elaboration not only in behavioural repertoires, but also in sensory systems. That is, evolving extensive abilities to use one sensory modality might be expected to impose constraints on the ability to use other sensory modalities. As with behaviour, we might expect to find especially pronounced evidence of adaptive tradeoffs in sensory specialisation among the arthropods. However, evidence is limited and tends to be contradictory.

In this thesis, I use salticids (jumping spiders) as a case study. The eyesight of most spiders is rudimentary, salticids being the primary exception. The salticid's complex eyes are structurally different from the eyes of any other animal and salticids have visual acuity that exceeds that of any other animal of comparable size. Not surprisingly it is vision that has been emphasised in the literature as being the dominant sensory modality used by salticids in prey capture and intraspecific communication.

In the early literature, interest in vision-controlled behaviour almost completely overshadowed interest in detailed study of any other sensory modality in salticids (Crane, 1949; Drees, 1952; but see Millot, 1946). However, it is now evident that most if not all salticids, despite having extraordinarily good eyesight, make extensive use of silkborne chemical cues, as well as vibratory communication, in mediating interactions with conspecifics (Jackson, 1992). Even prey capture may be mediated by tactile cues alone (Forster, 1982; Taylor et al, 1998). Also, recent studies have shown that salticids rely heavily on pheromones, especially in the context of courtship, mating and aggression (Jackson, 1987; Clark & Jackson, 1994a; Clark & Jackson 1995a, b). Ironically, more is currently known about pheromone use by salticids than for all other spider families put together (Pollard, et al 1987; Richman & Jackson, 1992). Yet the question of whether salticids also rely on chemosensory systems in the context of predation has been largely overlooked.

My objective in this thesis has been to investigate a poorly understood area of salticid

biology, the role of chemosensory systems in salticid predator-prey interactions. Two general hypotheses are considered: (1) salticids that have evolved prey-specific predatory behaviours for use against particular types of prey have tended also to evolve abilities to recognise chemical cues from those particular prey; (2) the frequency of injury and cannibalism during intraspecific interactions has been an important factor favouring the evolution of abilities to discriminate between chemical cues from self and other conspecifics.

Chapter 2 is a literature review outlining the theoretical background for my thesis. In Chapters 3 to 5, I consider the role of chemical cues in predator-prey interactions between Queensland Portia fimbriata (Doleschall) and other species on which it preys. Portia fimbriata from Queensland is unique among species and populations of Portia because it preys on spiders from other families, and on all the populations of Portia studied. It also uses prey-specific tactics to capture other species of salticids, and prefers other salticids as prey (Jackson & Blest, 1982a; Jackson & Pollard, 1996). Many salticid species are taken by Queensland P. fimbriata. However, the most common salticid in P. fimbriata's Queensland habitat is Jacksonoides queenslandicus Wanless (Jackson 1988). The hypothesis I consider is that the Queensland P. fimbriata has evolved reliance on chemical cues from this particular species of prey.

In Chapter 6, I turn to another type of salticid with an unusual prey. Most salticids prey primarily on soft-bodied insects such as flies and moths. Ants are generally avoided. However, there is a minority group, the myrmecophagic species, that use ant-specific prey capture behaviour and prefer ants to other prey (Li & Jackson, 1996b). In chapter 6, I investigate whether a myrmecophagic (ant-eating) salticid, Habrocestum pulex (Hentz), makes use of chemical cues from ants to detect prey.

In Chapters 8 and 9, the type of predation considered is cannibalism (i.e., instances

were the predator and prey belong to the same species). Portia is known to be exceptionally cannibalistic (Jackson & Hallas, 1986b). In these chapters, I study species of Portia in which levels of cannibalism vary and investigate the role chemical cues play in governing interactions between potentially cannibalistic conspecifics.

Chapter 10 is a general discussion. Returning to the question of adaptive tradeoffs, I consider the wider implications of the research in this thesis.

CHAPTER 2:

THEORETICAL BACKGROUND TO THESIS

In this chapter, I review a number of inter-related topics that are relevant to the studies in later chapters of this thesis.

1. Models of Instinctive Behaviour

The vast body of experimental, observational, and theoretical work by the European ethologists, especially K. Lorenz, W.H. Thorpe, N. Tinbergen and G. Baerands, generated the concepts and framework underlying modern studies of animal behaviour. Ethological ideas relating to instinctive behaviour have been particularly influential and controversial. Lorenz (1952) envisaged instinct as consisting of three parts: (1) appetitive behaviour; (2) activation of innate releasing mechanisms (singular IRM; plural IRMs); and (3) discharge of the consummatory act. According to Lorenz's model the IRM ensures that a behaviour is performed only when a particular combination of stimuli (the releaser or sign stimulus) is encountered (Thorpe, 1963; Eibl-Eibesfeldt, 1970; Lorenz 1981). For example, Drees (1952) used the ethological framework in his study of jumping spiders. He argued that male jumping spiders respond initially to almost any small object (in nature this could be a mate or a food item) by approaching it; following the initial approach, the salticid responds with either prey-capture behaviour (if the stimulus is a short-legged object) or courtship (if the stimulus is a long-legged object, with legs orientated ca. 25 degrees to vertical). In this example, attention to movement and shape appear to be critical for activating the IRMs of predatory behaviour.

Traditionally, the behaviour of "lower organisms" (a category which often appears to

mean all animals other than birds and mammals) has been envisaged as governed primarily by instinct, rather than intelligence and learning (Lorenz, 1952; Thorpe, 1963; Punzo, 1984). Lorenz (1937, 1952) argued that higher organisms acquire learned behaviours by "instinct-training interlockings", in which instinctive chains are modified by the addition of learned elements. According to Lorenz (1952) there is no sharp boundary between instinct and learning, but the behaviour of arthropods and other lower organisms is considerably less modifiable than that of birds and mammals. The traditional view that invertebrates are highly rigid in their behaviour is challenged not only by extensive recent work but also by largely under-appreciated older literature demonstrating that learning can have a large role in shaping the behaviour of invertebrates (Schnierla, 1951; Thorpe, 1963; Corning & Lahue, 1972; Alloway, 1973; Krasne, 1973; Van Alphen & Vet, 1986; Vet, 1988; Dukas & Real 1993).

Parasitoids provide striking examples of insects benefiting from experience by becoming more efficient at attacking their hosts (e.g., Dmoch et al., 1985; see Vet & Gronevold, 1990; Vet et al., 1990 for reviews). The ability of mantises to learn to recognise and avoid unpalatable prey provides another example. Juvenile preying mantises attack milkweed bugs on their first encounter, then release this unpalatable prey. Subsequent attacks also result in attack and rejection, but the time taken to reject unpalatable prey is shorter by half (Paradise & Stamp, 1991).

According to Lorenz's (1952) model, and earlier studies (e.g., Craig, 1918), when an instinctive activity has not been released for a long time, the animal's response threshold to sign stimuli is lowered. That is, the animal enters a greater state of readiness to perform a specific instinctive activity. When this happens, stimuli that only roughly approximate the sign stimulus, and previously were ineffective releasers, now elicit the instinctive action. Concurrently, behaviour consistent with what Craig (1918) called 'appetitive behaviour' (also

referred to as 'recurrent behaviour'; Sherrington, 1906) may be performed in conjunction with the falling threshold and passage of time. Appetitive behaviour can be envisaged as an effort by the animal to locate the appropriate sign stimuli. If the releasers for a particular behaviour continue to be absent, vacuum activity may occur (i.e., the instinctive behaviour may be performed in the absence of any sign stimulus at all). Often instinctive behaviour is structured in chains (N. Tinbergen, 1951), where performance of one instinctive act in response to a sign stimulus brings the animal into the presence of the next sign stimulus and so forth.

2. **Recognition of prey animals using search images.**

2.0 Search images for optical cues

Methods by which predators select prey may be envisaged as a continuum. At one extreme the predators may take disproportionately many of a particular type of prey largely because it concentrates searching in the particular locations (e.g., on ledges, rocks or leaves) where the prey is common. At the other end of the continuum, the predator may rely primarily on cues coming directly from the prey organism (L. Tinbergen, 1960; Edmunds, 1974). For predators that rely primarily on cues coming from the prey animal itself, there is an implication that the perceptual system of the predator is somehow tuned to the preferred prey. How this tuning is achieved becomes a central question. One of the most influential proposals has been the "search image hypothesis" (L. Tinbergen, 1960) which is an elaboration of the concept of search images as proposed by von Uexküll and Kriszat (1934). This hypothesis suggests that, after encountering a prey animal, a predator retains an internal picture or image based on a large number of the characteristics of the actual prey. It is argued that, by referring to this image, the animal can then find this important prey more efficiently. Implicitly, search images

are formed by learning the characteristics of common prey during encounters with those particular prey animals (Dawkins, 1971).

The impetus for L. Tinbergen's (1960) search-image hypothesis was his own work and a concurrent study (Mook et al., 1960) showing that birds prey on certain species of insects at higher frequencies than expected by chance. Additionally, there is a lag between a particular type of insect becoming common and the bird escalating its rate of preying upon this particular type of insect. L. Tinbergen concluded that the birds become more efficient at finding the particular prey species that were common prey because of heightened attention given to the cues coming from this particular type of prey.

Observing that a particular type of prey had to reach a threshold density before the birds appeared to form a search image for it, L. Tinbergen (1960) argued that birds were constrained in the number of search images that they could adopt at any one time. That is, a trade-off was envisaged between utilisation of previously formed search images for one prey animal and the adoption of additional search images. The idea seems to be that the animal, constrained by limited neural capacity, cannot simultaneously assimilate and use multiple search images. If this constraint did not apply, then we might expect to find search images not only for frequently encountered but also for infrequently encountered insects. Arthropods, having brains considerably smaller than that of a bird, might be expected to be even more constrained in ability to use search images, if arthropods use search images at all. In this thesis, one of my interests is in whether search images and related concepts are applicable to araneophagic spiders.

The search-image hypothesis has been supported by numerous studies on birds, including passerines (Clarke & Allen, 1968; Alcock, 1973, Pietrewicz & Kamil, 1979) and pigeons (Murton, 1971). Stickleback fish have also been shown to adopt search images

(Beukema, 1969). Examples from arthropods are much less frequent. The most convincing example may be the cabbage white butterfly (Pieris rapae Linnaeus), which appears to pay attention to certain critical optical cues from host plants. Rausher (1978) studied the oviposition sites used by cabbage white butterflies in the presence of two host plants, Aristolochia reticulata (which has broad oval shaped leaves) and A. serpentaria Linnaeus(which has long narrow leaves). The number of times that female butterflies approached and tasted (a chemosensory behaviour) these two plants over a 30-min period, was compared with the relative abundance of the two types of plants during the observational time. Results were bimodal, suggesting that the population of Pieris rapae females consisted of two groups, females that always oviposited on broad leaves and females that never did. Consistent with these conclusions, individual females were observed to have a tendency to oviposit on leaves of a single shape (broad or narrow). It was argued that optical cues relating to leaf shape are an important variable governing the selection of oviposition sites by the butterflies, and this was described by Rausher (1978) as an insect example of search image use. However, the more traditional way in which search images are used as a tool for prey detection appears not to have been studied in arthropods.

2.1. Alternative mechanisms related to search images

As an alternative to L. Tinbergen's (1960) search image hypothesis, Royama (1970) argued that birds may simply learn where to look for prey rather than learning the characteristics of the prey animal (see also: Dawkins, 1971; Gullford & Dawkins, 1987). That is, the prevalence of a particular prey in the predator's diet might be an artefact of that prey occurring at the location in which the predator has learned to search. Some other kind of evidence would be needed for showing that the prey, rather than the habitat was actually being

selected by the predator.

Alcock's (1973) study of red-winged blackbirds in the laboratory suggests that search images, as envisaged by L. Tinbergen, and learning of location may operate together. The testing apparatus was a "food maze", which was a box that had two rows of holes in the walls for presentation of food. Two types of food were used (meal worms and sunflower seeds). On day 1 and 2, the birds were allowed to forage on food of one type that had been evenly distributed throughout both rows in the box. On day 3 the birds hunted for 16 food items which were of the same food type as presented on the first two days. Food items were arranged so that eight were on the top row and eight were on the bottom row. Testing on day 4 was the same as on the third day, but half the food items were mealworms and half were sunflower seeds. Compared with the first day of testing, the birds found food quicker on the second day of testing, indicating that hunting performance improved with experience. On the third day, the birds found particular food items more quickly when these food items were in the same row that had held food items on the second day. When mealworms and sunflower seeds were presented simultaneously, the birds found the previously experienced food type quickest (i.e., the birds that had previously found sunflower seeds found sunflower seeds quickest regardless of the location of the sunflower seeds). These results show that both locational cues and cues relating to the food item itself are important. Therefore, learning to find prey by searching at a particular location does not exclude the possibility that the characteristics of prey within that location may also be learned.

Another alternative to L. Tinbergen's (1960) search-image hypothesis is that, instead of learning what to look for, the predator learns the optimal speed at which to search for prey (the search-rate hypothesis: Gendron & Staddon, 1983; Guilford & Dawkins, 1987). That is, having found a prey item while searching at a particular speed, the predator may continue to

search at that speed. According to this model, the predator's rate of searching is envisaged as a trade-off between the rate at which prey is encountered and the probability of prey detection per unit time. It is assumed that the faster a predator searches for something, the less accurate the search will be. Several broad predictions can be derived from the model: (1) the more cryptic a prey animal, the slower a predator will search for it; (2) if two species differ in how cryptic they are, the more conspicuous one will always be over-represented in the predator's diet; and (3) the rate of predation on a cryptic prey animal decreases when more conspicuous prey are available. An especially important implication of this hypothesis is that, regardless of search rate, equally cryptic prey animals should be taken at the same rate. That is, having chosen an optimal searching rate, the ability of a predator to find additional prey items should not suffer. This is the reverse prediction to the search image hypothesis.

However, the search rate hypothesis appears unable to account for some recent findings from experimental studies. For example, Plaisted & MacIntosh (1995) tested pigeons for ability to detect two equally cryptic targets on a checkerboard background. They found that, as performance in detecting the most common target increased, performance at detecting of the less common target decreased. This is contrary to a prediction derived from the search rate hypothesis: that, because both targets are equally cryptic, performance in detecting both targets should increase. An experiment by Blough (1979) also provided evidence against the search rate hypothesis. Blough (1979) conditioned pigeons to strike at letters superimposed on a video screen. Pigeons which struck at the "correct" stimulus (letter) rather than an incorrect stimulus shape (letter or number) were given food. For example, in one of a series of experiments, the targets used were a D and a U shape. Previous experiments had shown that the reaction time to D was less than to U, suggesting that to pigeons D is less cryptic than U. During the experiment, D and U were presented along with other (incorrect) stimulus shapes at

intervals of 2, 4 and 6 sec. According to the search rate hypothesis, we would expect that the accuracy with which birds selected U should decline more than the accuracy with which birds select D. However, Blough (1979) found that the accuracy with which birds selected D was reduced more for D than for U.

2.2 Search images for chemical cues

Initially the search image hypothesis was applied only to predators that were relying on optical cues when searching for prey. However, the search image hypothesis appears to be applicable also to animals that rely on chemical cues. That is, we might expect to find not only 'optical search images' (heightened attention to certain optical cues) but also chemical search images (heightened attention to certain chemical cues). A predator with a chemical search image is thought to retain a "neural activity pattern corresponding to a specific feature of the odour mixture" coming from the prey (Atema et al., 1980). When the predator adopts a chemical search image, it becomes predisposed to respond readily to particular odours or odour mixtures, which match the chemical search image. Except for the sensory modality, chemical and optical search images are comparable abilities of the predator.

For example, Atema et al. (1980) studied how captive tuna responded to water in which prey had previously lived. Responses were scored on a scale of 1-5 (5 being the strongest predatory response). The tuna were fed on surf smelt, a fish species that is not available as natural prey. Chemical stimuli ("rinses") were prepared by gently swirling 200 grams of uninjured freshly killed fish (prey) in 1 litre of seawater. The prey were either smelt or natural prey fish. These rinses were filtered and then frozen for later use in testing. During testing, seawater was circulated through the test arena. Rinses were introduced to testing tanks by

dropping them into the waterflow, and the tuna's behaviour was observed for the next 4 min. Initially, tuna responded more strongly when tested with rinses from natural prey rather than smelt. However, over the next month, this changed and responsiveness to rinses from surf smelt increased eventually becoming stronger than the response to natural prey. Although additional experimental work is needed, this suggests the tuna were learning the chemical characteristics ("odour") of their prey and forming search images for these odours. In this example, the relevant odours appear to be related to the amino acid mixture from the prey that dissolves into the rinse (Atema et al., 1980).

Chemical search images also appear to be important when crotalid snakes strike and then release their prey. Chiszar et al. (1985) tested cottonmouths (Agkistrodon piscivorus), which were allowed to strike a potential prey animal (fish or mouse). Once struck, the prey was removed. A control group of cottonmouths was not allowed to strike prey. During 70-min tests, cottonmouths which had been allowed to strike prey performed more tongue flicks than did cottonmouths in the control group.

It is known that the period during which chemical cues remain available to the cottonmouth's vomeronasal organ after striking prey is about 10 min (Chiszar et al., 1985), and cottonmouths used in this study remained responsive for about 70 min, suggesting that the cottonmouth neurally retained a memory trace or chemical search image of the odour cue.

In a second experiment a cottonmouth was allowed to strike a prey (fish or mouse). This prey animal was immediately removed, and then the snake was presented with a dead prey animal. The prey presented to the snake was either the same as presented earlier or different. The latency to grasp the dead prey was shortest if it was the same as the prey animal, which the snake had struck earlier (Chiszar et al., 1985).

Chiszar et al. (1985) proposed that striking prey caused something like an image of that

prey to be called up in the central nervous system of the snake. The image appeared to guide the post-strike searching behaviour of the snake. Post-strike searching behaviour is an important part of these snakes' predatory behaviour. These snakes strike prey, then release it. The prey animal flees, and it is re-captured after death. If the prey is out of sight, however, the snake must relocate it, and this is when search images tend to be important.

In crotalid snakes, experiments have shown that striking the prey provides the stimulus responsible for inducing adoption of the search image. This is important, as striking prey causes chemical cues to be tasted by the snake's vomeronasal organ. Melcher & Chiszar (1989) presented prairie rattlesnakes (Crotalus viridis) with mouse carcasses which had been coated in perfume and with control (coated with water only) mouse carcasses. The snake was allowed to strike a mouse (coated with perfume or not). Subsequently, these snakes were given simultaneous access to carcasses of both types. In 16 out of 20 tests, snakes took the carcass coated with the same liquid (perfume or water) as the mouse they had struck earlier.

2.3 Linking modalities

One interesting possibility that appears not to have been previously considered is that cues from one sensory modality may promote an alteration in an animal's attention to cues in another modality ("modality linkage"). For example, a visual predator might theoretically be stimulated by chemical cues to carry out a search using visual cues.

My thesis focuses on Portia fimbriata (Doleschall), a salticid spider with a highly evolved visual prey detection system. As a large proportion of this species' prey are other salticids, which also have good eyesight, sensitivity to chemical cues from prey salticids might be especially useful for P. fimbriata, giving P. fimbriata early warning to use its highly evolved visual system, to begin searching for its prey, before its prey's own highly evolved visual

system, is used to detect P. fimbriata. In the present thesis, I investigate the potential for this type of modality linkages in P. fimbriata.

2.4 Cognitive aspects of search image use

L. Tinbergen (1960) tied his search-image hypothesis tightly to the idea that it is learned features of common prey that influence the predator's subsequent behaviour. This emphasis on learning became conventional in the subsequent literature. However, emphasis on learning may have deflected discussion away from deeper implications about cognitive ability. Forming search images implies that the predator's attention is shifted and focused on cues from a certain type of prey. That is, the hypothesis implies that encountering cues from particular prey alters the predator's cognitive state in relation to this particular prey (i.e., the predator becomes primed to pay attention to cues from this particular type of prey). It is this shift in attention which L. Tinbergen referred to as a search image. Using search images, therefore, can be envisaged as a special category of a larger class of abilities, ability to use internal schemata (either innate or acquired through experience) to locate a particular type of prey.

Natricine snakes apparently rely on innate schemata. Burghardt (1966) tested a litter of 20 garter snakes (Thamnophis sirtalis) for responses to prey (redworms, Eisenia foetida (Savigny); minnows, Notropis atherinodes acuta) and non-prey (horsemeat; mealworms, Tenebrio molitor Linnaeus larvae). Tests were carried out by placing a cotton wool swab next to the snake and observing its response. When tested with cotton wool which had been coated with fish or redworm extracts, the snakes attacked. However, they did not attack cotton wool which had been coated with extracts of mealworms, horsemeat, or water. This suggests that inexperienced garter snakes can, on the basis of chemical cues alone, distinguish prey from

non-prey. Using the terminology that was common in ethological literature, this ability would be interpreted as based on innate releasing mechanisms and innate responsiveness to sign stimuli from particular types of prey. Strictly speaking, this is not precisely the same as a search image as focused responsiveness is innate not learned in this example. Additionally, the experiment on natricine snakes does not demonstrate an effect on searching behaviour as such, but merely the elicitation of prey capture behaviour. However, this and other such innate schemata have in common with learned search images an implication of attentional bias toward cues from especially important prey. That is, both have in common the potential to bias a predator's attention toward particularly important prey.

2.5 Perceptual learning models for the formation of search images.

L. Tinbergen's (1960) search image hypothesis, though influential, does not go very far in explaining mechanisms for search image use. L. Tinbergen (1960) documented that the birds he studied had a prey preference, and outlined a framework for understanding how that preference could be used in locating prey, but he did not propose in detail a mechanism for how preferences were formed. There were comments to the effect that search images involved a kind of learning, but little in the way of detail, and this is probably why subsequent studies have tended to be efforts to show whether or not experience is necessary when predators form search images for cryptic prey, rather than efforts to understand what the cognitive processes are by which search images are formed and used by predators.

Recently, however, Plaisted & MacIntosh (1995) formulated a detailed model of the cognitive processes underlying search images. This model is based on two hypotheses, one of which concerns how search images are acquired through learning ("perceptual learning

hypothesis") and the other of which concerns how search images, once formed, are used by the predator to find prey ("attention threshold hypothesis").

2.5.1 The perceptual learning hypothesis

The perceptual learning hypothesis (reviewed in detail by McLaren et al., 1989; Reid & Shettleworth, 1992) has similarities to earlier hypotheses by Rosenblatt (1958) and Broadbent (1964). It proposes a complex process by which a predator learns to associate particular stimuli from a prey animal with food. When exposed to prey, the predator is envisaged as sampling only a small subset of the total array of stimulus characteristics present and not necessarily the same set of characteristics is sampled in subsequent encounters with the prey. It is proposed that a memory trace, built from the stimulus array associated with that prey, is stored in the predator's central nervous system as a coded representation (i.e., the "image"). This image has a series of elements, taken from the various stimuli that impart upon the predator's sensory system. To make the image, the predator cognitively associates elements common to more than one encounter with the prey. With each exposure, the strength of associations between the elements becomes stronger. Association eventually becomes so tight that exposure to only a subset of the total stimulus set used to form the image will cause all the stimulus representations to be activated together. That is, exposure to any part of the total stimulus set causes the predator to respond as it would to the whole image. The predator is then rendered ready and able to respond to its preferred kind of prey.

2.5.2. Attention threshold hypothesis.

The psychology literature has tended to interpret search images as being associative

networks corresponding to a large number of the prey's characteristics (Plaisted & MacIntosh, 1995; Reid & Shettleworth, 1992). However, the issue of how many or how few of the prey's characteristics are represented in the predator's search image would appear to be a secondary issue. For the predator, what matters is that prey species can be differentiated from non-prey and from the prey's background (Bond, 1983; Dawkins, 1971). For making such discriminations, most of the characteristics of a prey animal are probably redundant for the predator. Bond (1983) argued that if a predator can remember a few critical characteristics, perhaps as few as one, then it may be able to find the prey more or less as efficiently as would be the case if the search image was based on a large number of the prey's characteristics. This supposition became the basis for Bond's (1983) "attention threshold hypothesis", which proposes that predators use two prey detection modes: (1) specific searching, in which predators look for particular characteristics that identify particular prey; and (2) general searching, in which the predator looks for any acceptable prey. Attention shifts from non-specific searching to searching for particular characteristics and leads to a temporary increase in the rate at which prey that have the searched-for characteristics are captured. The attention threshold hypothesis predicts that predators using specific characteristics will switch back to more general searching when the frequency of encounters with this particular prey type falls below a threshold level. On the whole, the attention threshold hypothesis is consistent with earlier ideas about search image formation, but it makes no claims about the role of learning and experience.

The perceptual learning hypothesis, which is based on postulating that predators can form associative networks, may be envisaged as most applicable to large animals, with large brains, especially vertebrates. Arthropods, having vastly smaller and less complicated nervous systems than most vertebrates, might be expected generally to lack the associative ability

needed for more than the most rudimentary forms of perceptual learning (see Broadbent, 1964; Wehner, 1997). It might be especially difficult for a small predatory arthropod to form associative networks representing a large number of prey characteristics. That is, we might expect the ability of an animal to store large numbers of associations to be constrained by the size of the nervous system, with smaller brains being able to form smaller numbers of associations. Therefore, we might expect to find predatory arthropods, if they use search images at all, to base their search images on only a small number of associations. A consequence may be that search images are formed by arthropods for only a few prey, and that the search images that are formed might tend to be less precise than those formed by vertebrates.

The attention threshold hypothesis represents a potential solution to the apparent problem of understanding how arthropods might use search images, as it describes a process by which the number of stimuli a predator needs to assimilate can be minimised.

3. **Sensory mechanisms of prey recognition in salticid spiders**

The visual system of jumping spiders (Salticidae) is, for spiders, unique. Most spiders have poor eyesight, but the acuity of salticid eyes exceeds that known for any other animals of comparable size, and rivals that of our own. Perhaps it is not surprising that salticids tend to be cursorial, diurnal predators. Optical cues pertaining to the size, shape and movement pattern of prey are known to be important in mediating visual prey recognition in salticids (e.g., Freed, 1984). The most extensive experimental work on prey detection in salticids was probably that of Drees (1952), who systematically altered the characteristics of model prey. Drees' most effective model for eliciting courtship had a centralised body and a series of legs

angled off from the body at about 25° from vertical. In contrast, models of highly varied shape elicited prey capture behaviour. However, size was shown to be important, with the salticid tending not to treat the model as prey unless it was of a size similar to that of the test spider.

We now know that salticid behaviour is considerably more variable and often more complex than implied by Drees (1952). Prey-recognition systems in many salticid species must be more than simply a matter of differentiating between prey and non-prey. This is illustrated especially by recent studies on araneophagic and myrmecophagic salticids (Jackson & Pollard, 1996).

4. **Araneophagic (spider-eating) salticids**

A wide range of salticids practise araneophagy by walking or, more often, leaping into the webs of other spiders and catching the resident (Jackson, 1986). More specialised araneophagy is practised by a smaller group of salticids. After entering another spider's web, these salticids do not merely stalk the resident. Instead, they manipulate the web silk with their legs and palps, making web-signals that deceive, and control the resident spider's behaviour (Wilcox & Jackson, 1998). For instance, these spiders may imitate the signals of a struggling prey insect or they may imitate the courtship signals of the resident spider. This predatory strategy is called "aggressive mimicry". Aggressive mimicry is known in only four salticid genera (Brettus, Cyrba, Gelotia and Portia) all of which belong to the subfamily Spartaeinae (Jackson & Pollard, 1996). The species in the genus Portia are the most extensively studied. Also, for one particular population of one species of Portia, P. fimbriata from Queensland, araneophagy away from webs is also important.

When the Queensland P. fimbriata encounters salticids away from webs, it uses a

tactic, called cryptic stalking (Jackson & Blest, 1982a), which is not used by any other species or populations of Portia (Jackson, 1992). When cryptically stalking a salticid, the Queensland P. fimbriata approaches by walking in an especially slow mechanical gait. If the stalked salticid should turn around and face P. fimbriata, P. fimbriata freezes and does not move again until after the prey salticid turns away. P. fimbriata's palps are retracted against the front legs when cryptically stalking. Palp outlines appear to be cues by which salticids recognise other salticids (Jackson & Pollard, 1996), and this posture appears to function to break up these outlines. Salticids are unusually common in the Queensland rainforests, and cryptic stalking probably evolved as a local adaptation for catching this locally abundant prey (Jackson & Blest, 1982a; Jackson & Hallas, 1986a).

5. **Prey-capture methods of myrmecophagic (ant-eating) spiders**

For spiders, ants might appear to make convenient prey, as they are the dominant prey-size arthropods in most habitats (Hölldobler & Wilson, 1970). However, strong mandibles, stings and other chemical defences (e.g., formic acid), plus being social insects that can mount communal attacks on predators (Hölldobler & Wilson, 1990), probably prohibit predation on ants by most spiders (Bristowe, 1941). Yet a large minority of spiders have overcome the ant's formidable defences. Reports of myrmecophagy in spiders are compiled in Table 1, but I make no pretence at it being complete, as reports of ant-eating tend to be difficult to locate, often being embedded in publications on other topics. As ants are well defended, myrmecophagy tends to be unexpected and therefore only rarely looked for. Though the level of relevant detail in the different reports that were located varies greatly, some trends do seem evident from the literature.

Especially many ant-eating spiders are web builders. Directly confronting the ant on the ground as a hunting spider without a web may tend to be more dangerous than web use for a spider. That is, webs may be important in facilitating predation on ants, as web silk is a tool by which spiders can overcome these especially dangerous prey. Not only might web silk ensnare an ant, but webs may also provide the spider with an optimal position from which to launch an attack. For example, web spiders may often attack by dropping down from the web on to an ant on the ground below (Shulov & Weissman, 1939; Shulov, 1940, 1966; Mathew, 1954; MacKay, 1982). As discussed by Robinson & Valerio (1977), potential advantages of this mode of attack include: (1) difficulty an ant might have defending itself against an attack from above; (2) communal defences being circumvented by plucking one ant off the ground before other ants can come to its assistance; (3) ants being impaired in their ability to detect spiders approaching from above. Web-building spiders often combine raising ants off the ground with another tactic, wrapping them in silk, which may make counterattacking difficult for ants (Fowler & Diehl, 1978; Culin & Yeargan, 1982; Nentwig, 1983).

There are especially many records of ant-eating by theridiids (reviews: MacKay, 1982; Nyffeler et al., 1988). Most but not all of these are for web-building theridiids. Some theridiids, for example, build webs over the entrances of ant nests, catching ants as they come out to forage (Hölldobler, 1970; Abalos, 1980; Clark, 1996). The common name for theridiids is 'comb-footed spiders', referring to a set of long setae (the 'comb') on the dorsal side of the tarsus and metatarsus of each leg IV. When attacking prey, theridiids use these combs to pull silk from the spinnerets and throw it over the prey. Being especially effective at wrapping prey may be an important factor in contributing to theridiids being successful ant predators.

Theridiid webs tend to have beads of fluid glue strung along web lines, with these lines being in locations prey are likely to intersect. Steatoda bipunculata Linnaeus (Bristowe, 1941),

Table 1. Spider species which have been observed feeding on ants

Family and species of spider[1]	Prey capture method	Ant predation frequency[2]	Reference
AGELENIDAE			
Agelena naevia Walckenaer	Uses ground-level web.	Occasional	Bilsing (1920)
Tegenaria atrica C.L. Koch	Uses ground-level web.	Routine	Bristowe (1941) Nentwig (1983)
Tegenaria ferriginea (Panzer)	Uses ground-level web.	Occasional	Nentwig (1983)
APHANTOCHILIDAE			
Aphantochilus rogersi O.P. Cambridge	Hunts without web. Ant-specific tactics. Uses deas ant as shield.	Routine	Oliveira & Sazima (1984) Castanho & Oliveira (1997)
ARANEIDAE			
Acanthepeira stellata Walckenaer	Uses aerial web.	Occasional	Nyffeler et al. (1988)
Araneus diadematus Clerck	Uses aerial web.	Occasional	Bristowe (1941)
Araneus trifolium (Hentz)	Uses aerial web.	Occasional	Bilsing (1920)

[1] Taxonomic status from Brignoli (1983) and Platnick (1989, 1993)

[2] Ant predators were divided into two broad categories: (1) occasional ant predators, those which probably prey on ants only when it is particularly safe to do so, or when there is no other food available (ants are less than 20% of the prey of these spiders); and (2) routine ant predators, those for which ants form a very high proportion of their prey (over 20% of the prey of these spiders), or those with ant-specific prey-capture behaviour (behaviour which is used only to catch ants).

Araniella cucurbitina Clerck[3]	Uses aerial web.	Occasional	Bristowe (1941)
Argiope argentata (Fabricus)	Uses aerial web.	Occasional	Nentwig (1985)
Argiope aurantia Lucas	Uses aerial web.	Occasional	Lockley (1995) Nyffeler et al. (1988)
Argiope savignyi Levi	Uses aerial web.	Occasional	Nentwig (1985)
Cyclosa turbinata (Walckenaer)	Uses aerial web.	Occasional	Nyffeler et al. (1988)
Eriophora bistriata (Rengger)	Uses aerial web.	Occasional	Fowler & Diehl (1978)
Eriophora fulginea (C.L. Koch)	Uses aerial web.	Occasional	Nentwig (1985)
Gea heptagon (Hentz)	Uses aerial web.	Occasional	Nyffeler et al. (1988)
Mangora gibberosa (Hentz)	Uses aerial web.	Occasional	Nyffeler et al. (1988)
Metepeira sp.	Uses aerial web.	Routine	MacKay (1982)
Metepeira seditiosa (Keyserling)	Uses aerial web.	Routine	Viera (1995)
Neoscona arabesca (Walckenaer)	Uses aerial web.	Occasional	Culin & Yeargan (1982)
Nuctenea umbratica Clerck	Uses aerial web.	Occasional	Bristowe (1941)
Zygiella x-notata (Clerck)	Uses aerial web.	Routine	Bristowe (1941) Nentwig (1983)
CORRINIDAE			
Castianeira spp. indet.	Hunts without web. Resembles ants.	Routine	Hingston (1927)
Corinna vertebrata Mello-Leitâo	Hunts without web. Hunts near ant nest. Resembles ants.	Routine	Fowler (1981) Fowler (1984)
CTENIZIDAE			

[3] Formerly Araneus cucurbitina

Cupiennius salei (Keyserling)	Hunts without web	Routine	Nentwig (1986)
DICTYNIDAE			
Phantyna segregata Gertsch & Mulaik[4]	Uses aerial web.	Occasional	Nyffeler et al. (1988)
DINOPIDAE			
Dinopis longiques F Cambridge	Throws net over ant.	Routine	Robinson & Robinson (1971)
DIPLURIDAE			
Ischnothele spp.	Uses trapdoor.	Occasional	Coyle & Ketner (1990)
DYSDERIDAE			
Harpactea hombergi (Scopoli)	Hunts without web.	Routine	Donisthorpe (1927)
ERESIDAE			
Seothyra henscheli Dippenaar	Uses ground-level web.	Occasional	Lubin & Henschel (1996)
GNAPHOSIDAE			
Callilepsis nocturna Linnaeus	Hunts without web. Hunts near ant nest. Ant-specific tactics.	Routine	Heller (1976)

[4] Formerly Dictyna segregata

HAHNIDAE			
Neoantistea spp	Uses aerial web.	Routine	Nyffeler et al. (1988)
LINYPHIIDAE			
Frontinella frutetorum (C.L Koch)	Uses aerial web.	Occasional	Herberstein (1997)
Linyphia triangularis Clerck	Uses aerial web.	Occasional	Bristowe (1941) Herberstein (1996, 1997) Nentwig (1983)
Neriene radiata (Walckenaer)	Uses aerial web.	Occasional	Herberstein (1997, 1998)
LIOCRANIDAE			
Phrurolithus claripes Dönitz & Strand	Hunts without web.	Occasional	Komatsu (1961)
Phrurolithus festivus (C.L. Koch)	Hunts without web. Resembles ants.	Occasional	Donisthorpe (1927)
Phrurolithus minimus Koch	Hunts without web. Resembles ants.	Occasional	Donisthorpe (1927)
LYCOSIDAE			
Alopecosa carinata Olivier	Hunts without web.	Occasional	Bristowe (1941)
Lycosa saccata Linnaeus	Hunts without web.	Occasional	Bristowe (1941)
Lycosa timuga Wallace	Hunts without web.	Occasional	Whitcomb et al. (1973)
OECOBIIDAE			

Oecobius annulipes Lucas	Uses silk to wrap ant.	Routine	Glatz (1967)
Oecobius cellariorum (Dugés)	Uses silk to wrap ant.	Routine	Glatz (1967)
Oecobius templi Cambridge	Uses silk to wrap ant.	Routine	Glatz (1967)
OONOPIDAE			
Triaeris patellaris Bryant[5]	Hunts without web.	Occasional	Weber (1957)
OXYOPIDAE			
Oxyopes salticus Hentz	Hunts without web.	Routine	Nyffeler et al. (1988)
PHOLCIDAE			
Pholcus phalangioides (Fuesslin)	Uses aerial web.	Routine	Nentwig (1983)
SALTICIDAE			
Aelurillus aeruginosus (Simon)	Hunts without web. Ant-specific tactics.	Occasional	Li et al. in press
Aelurillus cognatus O.P. Cambridge	Hunts without web. Ant-specific tactics.	Occasional	Li et al in press
Aelurillus kochi Roewer	Hunts without web. Ant-specific tactics.	Occasional	Li et al. in press
Chalcotropis sp. (6 species)	Hunts without web. Feeds on larvae.	Routine	Jackson et al (1998)

[5] Formerly Triaeris stenapsis

	Ant-specific tactics.		
Chrysilla lauta Thorell	Hunts without web.	Routine	Jackson & van Olphen (1992)
	Ant-specific tactics.		
Corythalia canosa (Walckenaer)[6]	Hunts without web	Routine	Jackson & van Olphen (1992)
	Ant-specific tactics.		Edwards et al. (1974)
Cosmophasis sp 1, sp2	Hunts without web.	Routine	Curtis (1988)
Euophrys sp. (2 species)	Hunts without web.	Routine	Jackson et al (1998)
Evarcha albaria (L. Koch)	Hunts without web.	Routine	It (1977)
Habrocestum pulex Hentz	Hunts without web.	Routine	Cutler (1980)
	Ant-specific tactics.		
Jacksonoides queenslandicus Wanless	Hunts without web.	Occasional	Jackson (1988)
Menemerus confusus Bosenberg & Strand	Uses web.	Occasional	It (1977)
	Ant-specific tactics.		
Myrmarachne 3 spp., indet.)	Hunts without web.	Occasional	Hingston (1927)
	Resembles ants.		
Myrmarachne foenisex Simon	Hunts without web.	Occasional	Wanless (1978a)
	Resembles ants.		
	Feeds on larvae.		
Natta spp (3 species)	Hunts without web.	Routine	Jackson et al. (1998)
Natta rufopictus (Simon)[7]	Hunts without web.	Routine	Jackson & Van Olphen (1992)
	Ant-specific tactics.		
Phidippus audax Hentz	Hunts without web.	Routine	Nyffeler et al. (1988)
Plexippus paykulli (Audouin)	Hunts without web.	Occasional	Edwards et al. (1974)
Plexippus setipes Karsch	Hunts without web.	Occasional	It (1977)
Siler sp.	Hunts without web.	Routine	Jackson et al. (1998)
Siler semiglaucus Simon	Hunts without web.	Routine	Jackson & Van Olphen (1992)
	Ant-specific tactics.		

[6] Formerly Stoidis aurata
[7] Formerly Natta horizontalis Karsch

Silerella vittata (Karsch)[8]	Hunts without web. Feeds on larvae.	Routine	It (1977)
Thiodina sylvana (Hentz)	Hunts without web.	Occasional	Edwards et al. (1974)
Tutelina similis (Banks)	Hunts without web. Ant-specific tactics. Resembles ants.	Routine	Denne (1982) Wing (1983) McIver (1987)
Zenodorus spp.	Hunts without web.	Routine	Jackson, unpubl.
Zenodorus orbiculatus (Keyserling)[9]	Hunts without web.	Routine	Jackson & Van Olphen (1991)
SEGESTRIDAE			
Segestria senoculata Linnaeus	Uses ground-level web.	Occasional	Bristowe (1941)
SICARIIDAE			
Loxosceles reclusa Gertsch & Mulaik	Hunts without web.	Occasional	Hite et al. (1966)
TETRAGNATIDAE			
Nephila clavipes (Linnaeus)	Uses aerial web.	Occasional	Herberstein (1997)
Metellina merianae Scopoli	Uses aerial web.	Occasional	Bristowe (1941)
Tetragnatha laboriosa Hentz	Uses aerial web.	Occasional	Nyffeler et al. (1988) Culin & Yeargan (1982)
THERIDIIDAE			

[8] Formerly Siler cupreus Simon
[9] Formerly Pystira orbiculata

Achaearanea sp. indet.	Uses aerial web.	Routine	Cullen (1991)
Achaearanea krausi Chrysanthus[10]	Uses aerial web.	Routine	Jackson unpubl.
Achaearanea lunata Clerck	Uses aerial web.	Routine	Bristowe (1941)
Achaearanea mundula (L. Koch)	Uses aerial web.	Routine	Jackson unpubl.
Achaearanea saxatile Clerck	Uses aerial web.	Occasional	Bristowe (1941)
Achaearanea tepidariorum (Clerck)	Uses aerial web.	Routine	Bristowe (1941)
			Nyffeler et al. (1988)
Argyrodes sp.	Uses aerial web.	Routine	MacKay (1982)
Argyrodes flavipes	Uses aerial web.	Occasional	Jackson, unpubl.
Dipoena sp. indet.	Uses aerial web.	Routine	Hingston (1927)
Euryopis acuminata (Lukas)	Uses silk to wrap ant.	Routine	Berland (1933)
Euryopis coki Levi	Uses silk to wrap ant.	Occasional	Porter & Eastmond (1982)
Euryopis californica	Uses silk to wrap ant.	Occasional	MacKay (1982)
Euryopis formosa Banks	Uses silk to wrap ant. Hunts near ant nest.	Occasional	Clark & Blom (1992)
Euryopis funebris (Hentz)	Uses silk to wrap ant.	Routine	Carico (1978)
Lactrodectus corralinus Abalos	Uses aerial web.	Routine	Abalos (1980)
Lactrodectus hesperus Chamberlain & Ivie	Uses aerial web.	Routine	MacKay (1982)
Lactrodectus mactans (Fabricus)	Uses aerial web.	Routine	McCook 1880)
		Routine	Gentry (1964)
		Routine	Nyffeler et al. (1988)
Lactrodectus mirabilus (Holmberg)	Uses aerial web.	Routine	Abalos (1980)
Lactrodectus quartus Abalos	Uses aerial web.	Routine	Abalos (1980)
Lactrodectus pallidus (O.P-Cambridge)	Uses aerial web.	Routine	MacKay (1982)
			Shulov (1940, 1966)
			Shulov & Weisman (1939)
Steatoda bipunctulata Linnaeus	Uses aerial web.	Occasional	Bristowe (1941)

[10] Formerly Achaearanea camura Simon

Steatoda fulva (Keyserling)	Uses aerial web. Hunts near ant nest.	Routine	Hölldobler (1970) MacKay (1982) Clark (1996)
Steatoda phalerata (Panzer)[11]	Uses aerial web.	Occasional	Donisthorpe (1927)
Steatoda pulchus	Uses aerial web.	Routine	MacKay (1982)
Theridion australe Banks	Uses aerial web.	Occasional	Nyffeler et al. (1988)
Theridion rabuni Chamberlain & Ivie	Uses aerial web.	Occasional	Nyffeler et al. (1988)
Theridion riparium Blackwell	Uses aerial web.	Occasional	Donisthorpe (1927)
Theridion sisyphium Clerck	Uses aerial web.	Occasional	Bristowe (1941)
Theridion tinctum Walckenaer	Uses aerial web.	Occasional	Bristowe (1941)
Theridion varians Hahn	Uses aerial web.	Occasional	Bristowe (1941)
Tidarren haemorrhoidale (Bertkau)	Uses aerial web.	Routine	Nyfffeler et al. (1988)
THOMISIDAE			
Amyciaea albomaculata	Hunts without web. Hunts near ant nest. Ant-specific tactics.	Routine	Cooper et al. (1990)
Amyciaea forticeps (Cambridge)	Hunts without web. Uses dead ant as shield	Routine	Shelford (1902 Hingston (1927) Mathew (1954)
Bucranicum sp.	Hunts without web.	Occasional	Bristowe (1931-1941)
Misumenops californicus	Uses web.	Occasional	MacKay (1982)
Misumenops coloradensis	Uses web.	Occasional	Hölldobler (1976)
Saccodomas formivorus	Uses web.	Routine	McKeown (1952)

[11] Formerly Asagena phalerata

Strophius nigricans Keyserling	Hunts without web. Uses dead ant as shield.	Routine	Olivera & Sazima (1985)
Xysticus sp.	Hunts without web.	Routine	MacKay (1982)
Xysticus sp.	Hunts without web.	Routine	Nyffeler & Breene (1990)
Xysticus cristatus	Hunts without web.	Routine	Nentwig (1986)
Xysticus erraticus Blackwell	Hunts without web.	Routine	Bristowe (1941)
Xysticus funestus (Keyserling)	Hunts without web.	Occasional	Nyffeler et al. (1988)
ULOBORIDAE			
Uloborus glomosus (Walckenaer)	Uses web.	Occasional	Nyffeler et al. (1988)
ZODARIIDAE			
Habronestes bradleyi Walckenaer	Hunts without web. Ant-specific tactics.	Routine	Allan et al. (1996)
Zodarion elegans	Hunts without web.	Occasional	Donisthorpe (1927)
Zodarion frenatum (Simon)	Hunts without web. Hunts near ant nest.	Routine	Harkness (1977) Harkness & Harkness (1992)
Zodarion gallicum (Simon)	Hunts without web. Resembles ants.	Routine	Boeve (1992)
Zodarion germanicum C.L. Koch	Hunts without web.	Routine	Schneider (1971)
Zodarion italicum (Canestrini)	Hunts without web.	Occasional	Donisthorpe (1927)

for example, has glue-covered lines extending down to the ground from aerial webs, and Achaearanea krausi Chrysanthus (Jackson, unpubl.) has similar lines that extend horizontally to tree trunks and boulders. These lines are strung under tension. When an ant walking along the ground, a tree trunk or a boulder contacts one of these lines, it adheres to the glue and begins to struggle. When struggling breaks the line, the released tension pulls the ant up from the ground or in from the tree trunk or boulder.

Silk lines may often function to alert spiders to an ant's presence, as illustrated by segestrids, eresids and other spiders. Segestrids extend ground-level silklines out from a tunnel, and ants that trip over these lines alert the spider, which then rushes out, seizes the ant and takes it inside the silk tunnel (Bristowe, 1941). The desert living eresid Seothrya henscheli Dipenaar uses sticky threads which are laid across sand to trap terrestrial arthropods that may be walking past. Rather than actively hunt for ants, the eresid waits in a burrow, or beneath a silk mat, then runs out and catches the trapped ant. Web-builders from a number of families descend down from their webs to attack from above when ants trip over ground-level silk lines (Bilsing, 1920; MacKay, 1982; Nyffeler et al., 1988; Cooper et al., 1990; Cullen, 1991).

Lacking webs, cursorial spiders may nethertheless use silk as an ant-capture tool. For example, Euryopis spp. are ant-eating theridiids that do not use webs to catch their prey. Instead, they either loop viscous threads around the ant (Carico, 1978) or else they use silk to tie the ant to the ground and then bite it on a leg (Porter & Eastmond, 1982). Subsequently, the ant is carried in a silk 'sling' attached to the spider's abdomen (Berland, 1933; Clark & Blom, 1982; Porter & Eastmond, 1982). Oecobius spp. (Oecobiidae; Glatz, 1967) resemble Euryopis spp. by using silk to wrap ants, but with some specialities of their own. The oecobiids first attach silk lines to the ant, then circle around the ant, rapidly applying a silk cover to it that renders the ant more or less defenceless.

Other spiders prey on ants without wrapping them or using webs. For these spiders, an element of surprise may be particularly important. One way that myrmecophagic spiders can surprise ants is by using aggressive mimicry (i.e., by resembling the ant on which it preys).

'Shielding behaviour' can be envisaged as a simple type of aggressive mimicry. By carrying a dead worker ant as a shield, the spider seems to disguise itself as a worker ant of the species on which it preys (Bristowe, 1941; Mathew, 1954; Oliviera & Sazima, 1984; Cushing, 1997). This allows the spider to get close enough to launch an attack on the ant which is being approached.

Shielding behaviour may also be interpreted as a type of ambushing, in which the predator's disguise keeps the ant unwary until it is close enough to be attacked. Other myrmecophagic spiders ambush ants without using a shield. Several spiders from the thomisid genus Amyciaea have ant-like behaviour and appearance. For example, Amyciaea albomaculata and A. forticeps (Cambridge) wave their first pair of legs in the air, apparently mimicking the movements of an ant's antenna.

A. forticeps has black spots on its abdomen. Mathew (1954) suggested that, as a consequence of these black spots combined with waving of legs, A. forticeps resembles a struggling ant so closely that nearby ants approach to help what they perceive as one of their conspecifics in distress. However, this hypothesis has not been tested experimentally. Ants on the whole have limited vision suggesting that optical features may not be important cues that cause ants to misidentify myrmecophagic spiders as other ants. Whether A. forticeps chemically mimics the ants on which it preys has not been investigated.

In fact, chemical mimicry of ants by spiders has only rarely been investigated at all (Allan et al., 1996). Optical and chemical resemblance need not vary together, and information on whether a spider chemically resembles ants is not as accessible to human observers as

information on optical resemblences tends to be. Perhaps chemical-based mimicry is widespread in myrmecophagic spiders. Only experimental studies can resolve whether or not this is so.

When using the term 'ant mimic' only for spiders that optically resemble ants, a trend appears. Most ant mimics tend not to be myrmecophagic, and most myrmecophagic spiders are not ant mimics (Reiskind, 1977; Elgar, 1993).

Staging ambushing attacks from above may be a common tactic of cursorial myrmecophagic spiders. Zenodorus orbiculatus (Keyserling), for example, is a salticid that positions itself on a tree trunk, remains quiescent and makes sudden lunging attacks on unwary ants that walk below (Jackson & van Olphen, 1991). Wing (1983) observed Tutelina similis (Banks), on a sage bush, stalking an ant moving about below. The ant was stalked slowly, then T. similis suddenly rushed toward the ant, attacking it from behind.

Some myrmecophagic cursorial spiders actively manoeuvre into a position from which to launch an attack from behind (Mathew, 1954; Wing, 1983; Oliviera & Sazima, 1984, 1985; Cooper et al., 1990; Jackson & van Olphen, 1991, 1992; Jackson et al., 1998). Attacks aimed at the rear of the ant may be advantageous in keeping the spider out of harm's way (away from the ant's mandibles). Another advantage may be that the spider's fangs contact the relatively soft cuticle on the ant's abdomen instead of the hard cuticle on the ant's head. Another tactic of myrmecophagic spiders is to approach from the rear and make attacks directed toward the soft cuticle of the upper surface of the thorax just behind the ant's head (Edwards et al., 1974; Wing, 1983; Oliviera & Sazima, 1985; Cooper et al., 1990; Li & Jackson, 1996b). Still other myrmecophagic cursorial spiders consistently make head-on attacks. The studied examples are all salticids (Jackson et al., 1998).

Sometimes the ant is grabbed by the soft thoracic cuticle just behind the head, then

lifted off the substrate. Held in this way, the ant cannot readily counter-attack (Oliviera & Sazima, 1985). Another factor may be that attacks aimed close to the ant's head (thorax just behind the ant's head) may be especially effective at immobilising ants as the venom may rapidly reach the central nervous system of the ant.

Rather than initially hold on and attempt to overpower an ant after attacking it, some myrmecophagic cursorial spiders bite or stab the ant, release it, and then wait at a safe distance for the venom to take effect (Heller, 1976; Harkness, 1977; Jackson & van Olphen, 1991, 1992; Jackson et al., 1998; Li et al., in press). This may be done repeatedly until the ant succumbs. When frontally attacking, stab-release tactics minimise the time an ant would have to retaliate.

6. **Specialisation on ants**

Whether ant-eating spiders are ant specialists tends to be a difficult question to answer, partly because the term 'specialist' has multiple meanings (Li & Jackson, 1996b). In relation to diet, a spider that feeds exclusively or entirely on ants has a specialised diet. Some ant-eating spiders are probably specialists in this sense, although extensive field data are generally lacking. Prey-capture behaviour adapted specifically to ants as prey, even if other prey are also taken, is another type of specialisation, and many spiders appear to specialise on ants in this sense. A spider that routinely takes not only ants but also other prey might nevertheless have a preference for ants over the other prey, and this is yet another way in which a predator might be an ant specialist.

Many spider species may take ants opportunistically, when it is safe to do so or when alternative prey is not available, but not be ant specialists in diet, preference or capture techniques. In determining whether a spider is an ant-specialist, the distinction between

preying on winged and non-winged forms of ants may be especially important. Some spiders may feed on winged ants (males and newly emerged queens) in much the same way as they would routinely feed on other prey (Nyffeler et al., 1988; Cushing, 1997). It is against the heavily defended workers that specialised tactics are likely to be needed, as the reproductive stages of the ants are comparatively defenceless. Besides adults, whether winged or not, the other ant stages on which spiders might prey are eggs, larvae, and pupae. Access to these stages might be rare for spiders. Although the literature is sometimes unclear on whether ant predation, when observed, was on workers or not, taking the eggs, pupae, and larvae of ants appears to be especially rare (It, 1977; Wanless, 1978a).

7. Cues by which ants are detected

Having acute vision, ant-eating salticids are of special interest. The most thoroughly studied myrmecophagic salticids are 11 euophryines (Corythalia canosa (Hentz), Habrocestum pulex, Zenodorus orbiculatus, 6 undescribed species of Chalcotropis and 2 undescribed species of Euophrys), seven heliophanines (Chrysilla lauta Thorell, Siler semiglaucous Simon, Siler sp., Natta rufopicta (Simon) and 3 undescribed Natta) and three aelurillines (Aelurillus aeruginosus (Simon), A. cognatus (O.P.-Cambridge), A. kochi Roewer) (Cutler, 1980; Edwards et al., 1974; Jackson & van Olphen, 1991, 1992; Li et al., 1996, in press). Each of these 21 myrmecophagic salticids also feeds on more typical insect prey such as flies and caterpillars, but uses different tactics depending on whether the prey is an ant (ant-specific prey-capture tactics) or a more conventional prey.

In ant-eating salticids, an ability to recognise ants by optical cues might be expected. However, even for salticids that are averse to ants, ability to discriminate ants from other insects on the basis of optical cues alone may often be advantageous, because ants appear to

be important natural predators of many salticid species (Jackson, unpubl.).

Despite the advantages of using optical cues to discriminate ants from other insects, situations may arise where it is in the salticid's best interest to detect chemical cues from ants. The potential for chemical detection of ants by salticids, however, has not been studied in detail. In this thesis, I present the results of a detailed investigation into how the predatory strategy of a myrmecophagic salticid, Habrocestum pulex, is influenced by chemical cues from ants (Chapters 6 and 7).

8. From pheromones to kairomones

Pheromones, chemical signals passed between different individuals belonging to the same species, are now known to be of widespread importance throughout the animal kingdom. However, it is in the insects that we find the most famous and most extensively studied examples. In insects, pheromones have many uses; for example, they can be used to mediate aggregation, deter oviposition, and function in sex recognition (Tamaki, 1985; Gabel & Thiéry, 1992; Baur et al., 1993; Barrera et al., 1994; Blaakameer et al., 1994, Bartelt & James, 1994; Dougherty et al., 1994; Hallet et al., 1995; McCall et al., 1996; Merlin et al., 1996). However, by using pheromones, the sender may have to contend with illegitimate receivers of the chemical message. For example, predators may locate prey by detecting the prey's pheromones, the prey's pheromone thereby serving as a kairomone for the predator.

A kairomone is defined as a chemical that reveals information which is beneficial to the receiver but not the sender of the signal (Brown et al., 1971). A clerid beetle, Thanasimus formicarius (Linnaeus), which is a predator of bark beetles, provides an especially clear example. T. formicarius is attracted to both naturally occurring (Wood et al., 1968) and

synthesised blends (Bakke & Kvamme, 1978, 1981) of the sex pheromones of its bark beetle prey (Ips typhographus (Linnaeus): Coleoptera, Scolytidae), these sex pheromones thereby being kairomones for the predator.

Kairomones are also known in arachnids, the most thoroughly studied being those of various predatory mites which are attracted to the aggregation pheromones of other species of mites on which they prey (Sabelis & Van der Waal, 1993; Koveos et al., 1995). Besides mites, the best-known arachnid order is Araneae, the spiders. In this group, kairomones have tended to be studied in less detail than other arthropods.

Kairomones form a sub-category of a larger category, allelochemics. Allelochemics are chemical signals exchanged between members of different species (Nordland & Lewis, 1976), and three subcategories are defined by how the use of the chemical cue affects the sender and the receiver. Kairomones help (i.e., increase the fitness of) the receiver but harm the sender. Allomones do the opposite: they help the sender but harm the receiver. Bolas spiders that simulate the sex attractant pheromone of their prey, male moths, are a famous example of allomone use in spiders (Eberhard, 1977). Synomones are beneficial to both the sender and the receiver. With pheromones, chemical signals exchanged between members of a single species, logically the same three sub-categories should be recognised, although a parallel set of terms is not usually adopted in the literature on pheromones. There is probably no need actually to create new terms. Perhaps it would suffice simply to accept that kairomones can be either allelochemics or pheromones. The same can be said to apply to allomones or synomones.

Although the use of kairomones by non-conspecific predators is well studied, particularly in insects, the problem of illegitimate detection of cues by members of the same species has not received much attention. The use of the word, kairomone, in reference to a

chemical used as a pheromone makes it easier to discuss instances where the cues detected were not intended to be transmitted in the first place: i.e., cues that are advantageous to the receiver but not the sender. One of my goals in this thesis is to consider instances of this type in salticid spiders.

9. Reliance on olfactory chemical cues by spiders

Initial studies of olfactory abilities of spiders were simple experiments in which volatile oils (e.g., lavender) were placed on a glass rod next to the spider, after which it was recorded whether the spider responded (Dahl, 1883, 1884; Peckham & Peckham, 1887, 1894; Pritchett, 1904). These studies sometimes showed that spiders could detect the volatile substances used, but how this ability might be useful in either communication with conspecifics or prey detection was not clarified. Often the responses seen in these early experiments might have been not a reaction to information provided by the cue but instead a more direct adverse reaction by the spider to a high concentration of potentially dangerous substances.

More recent studies have shown that spiders use olfactory chemical cues in mate attraction ('sex pheromones'). For example, Blanke (1973) demonstrated that Cytophora citricola Forskål (Araneidae) males can detect conspecific females held behind an opaque gauze bag with air flowing through it. Soon afterwards, Enders (1975) demonstrated in field tests that Argiope aurantia (Araneidae) females placed on a previously unoccupied bush attracted conspecific males within 15 min.

Olfactory chemical cues may also be relevant to predation. One of the most complete studies demonstrating the use of chemical cues in predation was conducted on an araneid spider, Cytophora citricola (Blanke, 1972). Prior experiments (e.g., Peters, 1931) had shown that vibrational cues from the wings of the ensnared insect are particularly important in

identifying prey. However, measurements of the wing beat frequency (Blanke, 1972; Sotavalta, 1963) show that the wings of flies and wasps beat at almost the same frequency, yet spiders appear to distinguish between flies and wasps. Flies are usually attacked and eaten, but wasps tend to be avoided.

Further experimentation showed that vibrational cues from the insect wings are not necessary. When Blanke (1972) removed the insect's wings, he found that C. citricola still avoided wasps. Additionally, if wasps were cut in half, separating the abdomen from the thorax, C. citricola still avoided each half, ruling out the possibility that the thoracic musculature that normally generates wing movement provided a cue. We might expect that, when vibrational cues are not used to identify prey, then visual cues might be important. However, araneids have only simple eyes and their rudimentary eyesight (Homann, 1971) is unlikely to be of any use in distinguishing flies from wasps. Additionally, flies which had been painted with yellow stripes to mimic wasps were still readily captured by C. citricola (Blanke, 1972). None of these experiments explicitly demonstrate that C. citricola uses chemical cues to identify prey, but taken together they strongly suggest chemical cue use.

More recently, Habronestes bradleyi Walckenaer, an ant-eating zodariid spider, has been shown to exploit volatile alarm pheromones from the ants on which it preys. Using an Y-shaped olfactometer, Allan et al. (1996) showed that H. bradleyi is attracted to air blown across injured or disturbed ants. However, there was no evidence of attraction when the experiment was repeated using undisturbed ants. Additionally, repeating the olfactometer tests using a synthesised version of the ant's alarm pheromone was successful in showing attraction. The ants used in this study, Iridomyrmex sp., use a ketone, 6-methyl-5-hepten-2-one as an alarm pheromone (Bergström & Lövqvist, 1970; Blum, 1981). The study by Allan et al. (1996) demonstrates that this ketone is a kairomone for Habronestes bradleyi. Interestingly, 6-

methyl-5-hepten-2-one is found in several genera of ants; (Lasius; Bernardi et al., 1967; Bergström & Lovqvist, 1970; Formica; Duffield & Brand, 1970; Iridomyrmex; Cavill et al., 1956; Bergström & Lofqvist, 1968; Allan et al, 1996; Turker, 1997; Conomyrmex; McGurk et al., 1968; Tapinoma; Trave & Pavin, 1956). An ant-eating spider might potentially detect several species using sensitivity to this one chemical, or to other chemicals which are structurally related to it. As no comparable studies have been carried out previously to determine whether ant-eating salticids react to ketones, this became one of the objectives of my thesis.

10. **Reliance on contact chemical cues by spiders**

In spiders, chemical cues seem to be especially often associated with silk. The silk may be web or nest silk, but especially often it is the spider's draglines. Draglines, which are lines of silk routinely trailed behind the spider as it walks about, are characteristic of spiders. Many, perhaps most, spiders leave draglines in the course of normal locomotion. Pheromones associated with draglines and nests are important in many, if not all, salticid spiders. It is especially common for nest or dragline silk of salticid females to elicit courtship from conspecific males (Jackson 1987; Clark & Jackson 1995a).

Silk-associated chemical cues may also prime males to more readily respond to optical cues from females (Crane 1949; Pollard et al. 1987). Two especially detailed studies illustrate this. Miyashita & Hayashi (1996) studied priming pheromones in Nephila clavata L. Koch (Tetragnathidae). They found that in the first 24 h after moulting, females produced a pheromone which both attracted males and primed them to initiate physical contact with the female. By washing newly moulted females in acetone, they extracted chemicals from the females cuticle. Test cages were prepared by allowing a female which had moulted 24 h

previously to build a web in a small box at one end of an olfactometer. After this a dummy female (a subadult which had been killed recently) was placed in this web, and a small piece of filter paper with acetone extract was placed beneath the web. The test male was then introduced to the olfactometer, and its behaviour observed. Control tests without odours present elicited a response from 20% of test males. However, when extracts from newly moulted females were present, all males moved toward and touched the female.

Yoshida & Suzuki (1981) showed that dragline-based chemical cues have a priming effect on Carrhotus xanthogrammus (Latrielle) (Salticidae) males. In experiments, males of this salticid were introduced into an area in which there were four artificial trees comprised of small branches. Each tree had on it a dead female mounted in a life-like posture ("model"). Prior to the experiment, females were allowed to walk over two of the trees, leaving behind draglines. The test began when the living female was removed and the male introduced to the area. Males walked more slowly when on the trees over which females had previously walked. Also, males courted the models made from dead females when on trees over which females had previously walked, but not when on untreated trees. It would seem that the female's pheromone stimulates the male to search in the vicinity of her draglines and primes the male to court when the appropriate optical cues are encountered. This experiment shows two different ways in which pheromones operate: as cues for mate location or as stimuli that prime males to respond to the optical cues that elicit courtship displays.

Priming pheromones, cues that prepare an animal to carry out particular tasks, are perhaps better known from studies of mammals rather than arthropods (MacDonald et al. 1990). For example, the odours from conspecific males of laboratory mice influence the timing of oestrus and reproduction (Whitten, 1958, 1959), the onset of puberty (Vandenburgh, 1969) and litter size (Zhiquin & Vandenburgh, 1992).

In araneophagic salticids, olfactory cues from conspecifics have been shown to inhibit aggressive-mimicry signalling (Wiley & Jackson, 1993). An unseen conspecific is likely to be dangerous and the olfactory cue appears to over-ride the araneophagic salticid's attention to the prey and instead switches attention to the possible attack by an unseen conspecific. Although this appears to be a priming effect relevant to predation, the chemical cue is still from a conspecific. Whether chemical cues from prey have priming effects on salticid behaviour appears not to have been investigated.

11. **Chemical signposts**

There is considerable literature on how animals use signpost cues in communication (i.e., cues left by an animal in the environment to be detected by other conspecifics). Signposts have the advantage that the sender does not have to be present for the signal to work. The most familiar signposts are probably the territorial scent markers of mammals (Hediger, 1952; Brown & MacDonald, 1985; MacDonald et al., 1990) which may especially often be sources of information on territory ownership and individual identity (Halpin, 1986). Invertebrates are known to use signposts in a way which is analogous to territorial signposts. For example, plant-feeding insects may leave signposts on host plants to deter other conspecifics from ovipositing on them (e.g., Barrera et al., 1994, Blaakameer et al., 1994; see Tumlinson et al., 1992 for a review).

Signals are typically envisaged as stimuli left deliberately by the sender (i.e., they are envisaged as an evolved adaptation with a communication function which is beneficial for the sender). In situations of intraspecific conflict, often deceptive use of signals (i.e., cheating) would seem to be advantageous to the sender. However, the potential for the evolution of

cheating by the sender may be constrained by the evolution of a tendency on the part of the receiver to respond to signals only if they are reliable (Hasson, 1994; Johnstone, 1997). For example, in a territorial animal, we expect there to be a link between signals being used in territory defence and the signalling animal's ability or willingness to fight effectively. However, it is unclear how signpost signals would be constrained against bluffing (i.e., cheating). With the sender no longer in close proximity to the signpost signal, there would seem to be no way for the receiver to check on the signal's reliability. Here the opportunity and advantage of cheating appears especially strong. Despite this theoretical problem, there appear to be examples of animals leaving signposts that do sometimes reliably reveal information about the fighting ability to rivals (Mathis, 1990; Hurst, 1993; Mathis & Simon, 1994; Drickamer, 1992).

Early studies (Jones & Nowell, 1973, 1974; Mainardi & Pascali, 1982; Parmigani et al., 1982a, b) demonstrated that females of two unidentified species of mice prefer to socialise with dominant rather than subordinate male mice. However, the role of signpost chemical cues was unclear because the male was actually present during testing.

Later the relevance of signpost chemical cues in communicating dominance was clarified by Sandnabba (1986a, b) who showed that mice of both sexes can use cues from urine to assess the dominance status of conspecifics. Urine from a highly aggressive mouse strain (TA) and from a less aggressive strain (TNA) was applied to the fur of castrated male mice. Mice with an intermediate level of aggression (NMRI mice) were more aggressive toward castrates scented with TA urine rather than TNA urine. Additionally, the mean attack latency was longer if castrated opponents were on bedding soiled by TA males, rather than on bedding soiled by TNA males (Sandnabba, 1986a). Simultaneous choice tests were also conducted (Sandnabba, 1986b), with mice being given a choice between clean bedding and bedding from cages that had previously contained TNA or TA mice. TNA males avoided areas

soiled by TA males, but TA males were attracted to bedding soiled by other TA males.

More recent experiments have shown that female mice use chemical signposts to determine the dominance status of males independent of the strain of mouse (Hurst, 1993; Drickamer, 1992). Drickamer (1992) tested the response of oestrus female house mice (Mus domesticus Rutty) to: (1) bedding from cages containing dominant or subordinate male mice (contact chemical cues); (2) odours from dominant or subordinate mice (olfactory chemical cues; tested using an olfactometer). Female mice preferred odours from dominant males in both types of test. Similarly, female cockroaches have also been shown to prefer odours from dominant males over odours from subordinate males (Breed et al., 1980).

Hurst (1993) added small quantities of urine to signposts which were normally in the environment of another species of house mouse (Mus musculus domesticus Schwarz & Schwarz). This new urine was investigated by residents, but the extent to which the new signpost was investigated was related to the status of the resident and donor mouse. Dominant males investigated urine from any subordinate mouse (either unfamiliar or familiar) more often than any subordinate mouse did. The effect of new urine signposts on how mice responded to conspecifics was particularly interesting. During these tests, animals from other cages were added in addition to those mice which were normally housed in that cage. Introduction of a new signpost containing urine from a subordinate resident caused the dominant resident male to increase its aggression toward all subordinates and the degree to which this happened was directly correlated with levels of aggression before the signpost was introduced. New signposts from unfamiliar subordinates caused an increase in the time spent investigating signposts, but did not cause an increase in levels of aggression toward subordinate mice. Subordinate males showed an increased tendency to flee from other mice if signposts containing urine from the dominant resident was introduced to the cage. However,

there was no significant change in the level of response of subordinate males when urine from unfamiliar dominant males or neighbouring males was introduced to the cage. These results show that urine from conspecifics reveals information about the familiarity of the signaller and the dominance status of the signaller. Additionally, urine from conspecifics has a priming effect (i.e., it increases the aggression level of dominant males toward subordinates, and it causes subordinate mice to flee). However, since the mice were present during testing, the role visual cues from the mice played in these discriminations is not clear. Additionally, these experiments demonstrate a strong effect on responses caused by familiarity, raising questions about the importance of information about dominance, per se.

Perhaps the most remarkable findings on chemical signposts come from salamanders. Recent studies (Mathis, 1990; Mathis & Simon, 1994) show that red-backed salamanders (Plethodon cinereus) respond differently to chemical signposts depending on the relative size of the conspecific that left the signpost. In response to chemical signposts from conspecifics, dominant salamanders are more prone to tapping their noses on the substrate than submissive salamanders (Mathis, 1990), suggesting that salamanders reveal their fighting ability (often referred to as RHP; resource holding power; Parker, 1974) with the signpost.

Although it has not been confirmed with staged contests that the larger salamanders have greater fighting ability, size is known to be a reliable indicator of fighting ability in many animals (Huntingford and Turner, 1987). In the absence of factors that guarantee the signal's accuracy, we might expect natural selection to favour individuals that bluff by leaving a signpost advertising higher RHP than they actually have. What guarantees that the signal is reliable?

A communication system may be envisaged as being based on a minimum of two individuals: the individual that makes a signal ("sender") and at least one individual who detects

and responds to the signal ("receiver"). The sender's and the receiver's interests are not necessarily the same (Dawkins & Krebs, 1978). For the receiver, it is important that the message conveyed by the signal is accurate, but deceitful messages might be advantageous for the sender. Something akin to an arms race might arise, with senders evolving to become better and better at deceit and receivers evolving to become better and better at protecting themselves against the problem of being deceived (Dawkins & Krebs, 1979).

"Probing" is one tactic by which a receiver might defend itself against bluffing (deceit). Probing is when receivers occasionally seek out the sender and actively test the ability of the sender to defend the resource over which the receiver and the sender are in conflict. However, for probing to work, the receiver must be able to find the signaller (sender), which is why signpost signals may be problematic. Another consideration is that the sender may not be limited simply to one of two tactics-- to be truthful or to bluff. More complex tactics may prevail in which animals only occasionally or intermittently exaggerate signals pertaining to RHP (e.g., size), thereby making detection of bluffing more difficult for the sender. Bond (1989) mathematically modelled the occurrence of bluffing in animals and argued that selection against bluffing was important only if bluffing occurred above a frequency of ca 20 %.

Caldwell's (1986; see also, Adams & Caldwell, 1990) studies on stomatopods appear to be consistent with Bond's (1989) model. Stomatopods are crustaceans which use their raptorial appendages as weapons and their tail as a shield. Tail size is an important cue by which agonistic interactions are settled. Bigger stomatopods tend to have longer tails and bigger, stronger raptorial appendages. Stomatopods live in cavities in coral or other hard substrates. Good-quality cavities are rare and stomatopods engage in intense contests to get them. As stomatopods moult throughout their life, proximity to moulting is an important factor mediating intraspecific interactions. Newly-moulted stomatopods are weaker than usual, but

can still spread their tails out. Despite having large raptorial appendages and tails, the newly moulted stomatopod actually is not especially dangerous because of its cuticle. Yet these individuals can still spread out their tails when an intruder threatens. Newly-moulted stomatopods seem to use the size of their tail to advertise that they are more capable of defending themselves than they really are. If the resident has a larger tail, indicating that it is stronger, the intruder is in a bind, as there is no way for the intruder to assess the fighting ability of the resident without entering the cavity. Compared to the resident, the intruder is more vulnerable as it is out in the open. Additionally, the intruder entering a cavity will not be able to use its tail as a shield for its head. The resident, by contrast, is in a small poorly lit hole, a position from which it can easily shield itself with its tail. Normally, the large tail would indicate that the intruder would be defeated, and perhaps seriously injured. It is, therefore, potentially more favourable for the intruder to assume that the tail size is an accurate reflection on the fighting ability of the resident, rather than to attack the resident. Encounters with recently moulted stomatopods are infrequent, and this may be why recently moulted stomatopods can get away with bluffing.

12. **Indirect assessment of fighting ability**

Alternatively, rather than an animal assessing the fighting ability of its rivals, the animal may use information about itself to make predictions about the likely outcome of a contest. For example, an animal that has had past experience of frequently winning fights may assess itself as a good fighter and escalate contests frequently because it expects to win. This is known for spiders, perhaps the most detailed study being Whitehouse (1997) who trained male Argyrodes antipodiana (Theridiidae) to lose or win contests. Winners were trained by always pairing them against smaller spiders; losers were trained by always pairing them against larger

spiders. Next equal size spiders were tested together. Whitehouse (1997) found that trained winners were more likely to escalate contests than trained losers. Prior experience evidently influenced the spider's assessment of its own fighting ability.

Another way an animal might assess its own fighting ability is by comparing its size with that of other conspecifics in the general population. If an animal frequently meets larger conspecifics, then it is informed that it is likely to be smaller than most of its potential rivals. Since size tends to be a reliable indicator of fighting ability in most animals (reviews: Archer, 1989; Huntingford & Turner, 1987), the optimal tactic for an animal that perceives itself as smaller than most conspecifics in the population might be to anticipate losing conflicts with any rival it encounters. These individuals might be expected either to minimise the level of escalation or to avoid fighting altogether.

12. **Self Recognition**

Another way in which animals might minimise agonistic conflict is to avoid encountering conspecifics. "Self recognition" refers to the ability of an animal to discriminate between cues from itself ("self") and those that come from other conspecific individuals ("nonself") (Parr, 1937). Although there appears to be numerous examples in vertebrates (Brown & MacDonald, 1985; Graves & Halpern, 1991), self-recognition has not been a traditional topic in studies on invertebrates (see Brace, 1990; Kawamura et al., 1991).

At least one species of salticid spider, Portia labiata (Thorell) from Sri Lanka, is capable of self recognition based on chemical cues. When given a choice, these spiders tend to remain in areas covered by their own draglines, rather than those covered by draglines from another conspecific. Additionally, P. labiata uses chemical cues to distinguish its own eggsac from the

eggsacs of conspecifics. There is no evidence for self recognition ability in two less cannibalistic species of Portia which were tested. It has been suggested that high levels of cannibalism have been responsible for the evolution of pronounced self-recognition abilities in P. labiata (Clark & Jackson, 1994a). In the present thesis, I extend this early work by testing for self recognition ability in species of salticid from genera other than Portia.

13. **Thesis objective**

My objective in this thesis is to investigate the influence of chemical cues on interspecific and intraspecific predatory behaviour in salticid spiders.

CHAPTER 3:

KAIROMONES FROM JACKSONOIDES QUEENSLANDICUS MEDIATE SALTICID-SPECIFIC PREDATORY BEHAVIOUR IN PORTIA FIMBRIATA, AN ARANEOPHAGIC SALTICID SPIDER

ABSTRACT

Portia fimbriata, an araneophagic salticid from Queensland, responds to both olfactory and contact chemical cues from Jacksonoides queenslandicus, an abundant salticid on which P. fimbriata preys. Laboratory experiments reveal three distinct effects: (1) attracting P. fimbriata to, or inducing P. fimbriata to remain in, areas where there are cues from J. queenslandicus; (2) changing P. fimbriata's behaviour in ways that facilitate prey capture; (3) enhancing P. fimbriata's attention to optical cues from J. queenslandicus. No statistical evidence was found that odours from other prey species have these effects on P. fimbriata, nor was evidence found to indicate that J. queenslandicus detects chemical cues from P. fimbriata. Portia fimbriata more often retracted its palps when on draglines from J. queenslandicus than when in clean cages. However, there was no statistical evidence that P. fimbriata retracted its palps more often when on draglines from Tauala lepidus than when in clean cages. Portia fimbriata began stalking J. queenslandicus lures, but not other lures, significantly sooner in cages where there were J. queenslandicus draglines than when in cages without J. queenslandicus lures. There was no statistical evidence that draglines from species other than J. queenslandicus affected latencies to begin stalking lures made from any species. Olfactory cues from J. queenslandicus also affected P. fimbriata. When tested in an olfactometer, P. fimbriata went into areas where there were odours from J. queenslandicus more often than into control areas (clean air). Sensitivity to chemical cues from J. queenslandicus appears to be specific to Queensland P. fimbriata, as there was no evidence of J. queenslandicus detection in experiments using another

species of Portia and another population of P. fimbriata provided.

INTRODUCTION

Most spiders have simple eyes and only rudimentary ability to discriminate shape and form, but salticids have complex eyes, acute vision and intricate vision-guided prey-capture behaviour (Land 1969, a, b; Forster, 1982; Blest et al., 1990; Jackson & Pollard, 1996). However, a highly evolved visual system, despite its many advantages, appears not to have precluded salticids from making use of chemical cues from conspecifics. Reliance on chemotactic and olfactory pheromones, particularly in the context of courtship and mating, is widespread not only in spiders that lack acute vision (Kaston, 1936; Millot, 1945; Robinson, 1982; Tietjen & Rovner, 1982, Trabalon et al., 1997) but also in salticids (Bristowe, 1941; Crane, 1949; Pollard et al., 1987; Jackson & Pollard, 1997; Taylor, 1998). Considerably less is known about how chemical cues might influence the predatory behaviour of salticids and other spiders (see Blanke, 1972; Persons & Uetz, 1996).

Ability to detect prey-derived chemical cues may be especially advantageous when prey are dangerous. Small, soft-bodied and more or less harmless insects may predominate in the diet of most salticids (Richman & Jackson, 1992). However, the salticid genus Portia is exceptional, as all Portia species studied (Jackson, 1992a) are versatile predators with a preference for other spiders as prey (Li et al. 1998). These remarkable salticids not only hunt away from webs but also build prey-capture webs and make predatory raids into other spiders' webs where they may eat the resident spider's eggs, the resident spider and ensnared insects. Spiders in alien webs are not simply stalked or chased down, but instead deceived and manipulated by aggressive mimicry signals prior to being attacked (Jackson & Wilcox, 1998; Wilcox & Jackson, 1998). As an additional

refinement, the Queensland P. fimbriata (Doleschall) takes salticids in preference to other types of spiders (Li & Jackson, 1996a).

When preying on salticids, the Queensland P. fimbriata uses a special tactic, called "cryptic stalking", which includes retracting palps back beside the chelicerae, thereby obscuring their outlines. The Queensland P. fimbriata also adopts a slow, mechanical gait and freezes whenever the salticid being stalked turns around to face the predator (Jackson & Blest, 1982a). Although many species of salticids are present in the Queensland rain forest, Jacksonoides queenslandicus Wanless appears to be by far the most abundant salticid on tree trunks, boulders and rock walls in the microhabitat of P. fimbriata (Jackson, 1988). Jacksonoides queenslandicus rarely defends itself against cryptically stalking P. fimbriata, but often flees or attacks a P. fimbriata that has not begun cryptic stalking (Jackson & Blest, 1982a; Jackson & Hallas, 1986a). The abundance of J. queenslandicus suggests local adaptation by P. fimbriata to this particular prey, a hypothesis we investigate by using Portia from sites where J. queenslandicus is not found: P. fimbriata from the Northern Territory of Australia and P. labiata from the Philippines.

In encounters between P. fimbriata and J. queenslandicus, being the first spider to detect the other's presence might be especially advantageous. Ability to detect kairomones (defined as chemicals that provoke a response beneficial to the receiver but not the sender of the signal, where the sender and receiver belong to different species; Brown et al., 1971) might provide a critical source of advance warning of the other salticid's presence. The early warning provided by detecting chemical cues from P. fimbriata could give J. queenslandicus time to flee or take other precautions against attack by P. fimbriata. Conversely, preparation by P. fimbriata for an encounter with an unseen J. queenslandicus might be important in lessening the likelihood of J. queenslandicus escaping. Safety may also be a factor for P. fimbriata because J. queenslandicus preys not only on insects, but also on spiders (Jackson, 1988). Whether P. fimbriata becomes J. queenslandicus'

prey, instead of vice versa, may depend on which spider sees the other first.

Salticids routinely lay down silk draglines while walking about in the environment (Foelix, 1993). Dragline-associated pheromones are known to elicit courtship in both P. fimbriata and J. queenslandicus (Jackson, 1987; Pollard et al., 1987), and to facilitate mate location in P. fimbriata (Clark & Jackson, 1995a). We investigate here whether J. queenslandicus avoids regions where there are draglines from P. fimbriata. We also investigate whether draglines from J. queenslandicus encourage P. fimbriata to remain in regions recently occupied by J. queenslandicus and to adopt elements of cryptic stalking. Whether P. fimbriata can locate J. queenslandicus using olfaction is investigated using an olfactometer, and we examine whether dragline-associated and olfactory cues influence P. fimbriata's attention to optical cues from prey.

Jacksonoides queenslandicus neither builds webs nor practises aggressive mimicry, but does enter the webs of other spiders (Jackson, 1988). Araneophagy is practised by leaping from outside onto spiders in webs, or by walking into a web and chasing down the other spider. Dead leaves and other detritus in webs are often adopted by J. queenslandicus as nest sites. Jacksonoides queenslandicus' affinity for webs provides an opportunity for P. fimbriata to make use of web-based predatory attacks on this salticid. One of our objectives is to investigate how chemical cues might influence these sequences.

We might expect responses to kairomones to be species specific and restricted to especially common prey. By testing P. fimbriata not only with J. queenslandicus, but also with other less common prey, we examine whether P. fimbriata's predatory responses to J. queenslandicus are specific to this particular prey or generalised responses to a wide range of prey.

GENERAL METHODS

Standard procedures for spider maintenance and rearing were adopted, as detailed elsewhere (Jackson & Hallas, 1986a). Spiders were maintained in a controlled-environment laboratory. All testing was during the morning and early afternoon (laboratory photoperiod 12L:12D, lights on at 0800hrs). Because choice-test procedures were in basic respects as described elsewhere (Clark & Jackson, 1994a, 1995b), only essential details and modifications relevant to the present study are provided here. All spiders used (Table 1) were adult females taken from laboratory culture (reared from eggs), and no test spider was used in more than two trials per experiment.

In addition to Queensland P. fimbriata, we also used P. fimbriata from the Northern Territory (Australia) and P. labiata from Sri Lanka as test spiders. Except when stated otherwise, 'P. fimbriata' always refers to the Queensland population.

Data, being skewed and of unequal variance, were analysed using non-parametric statistics (Sokal & Rohlf, 1995), adjusted using Bonferroni corrections (Rice, 1989) when multiple comparisons were made.

EXPERIMENT 1. DRAGLINE-CHOICE TESTS

Methods

To collect draglines, a source spider (Table 1) was placed in a new clean petri dish (diameter 90 mm) in which there were two circular pieces of blotting paper (diameter 90 mm), one taped to the inside top and one taped to the inside bottom of the dish. Each spider was left in the petri dish for 2 h, during which time it was seen to walk about and leave draglines on the paper.

After dragline collection, the two circles of blotting paper from the source spider's cage

Table 1. Spider species used as test spiders (T), source spiders (S) & lures (L) (see text).

Species	Abbreviation	Family	Origin[1]	Experiments	Use
Jacksonoides queenslandicus Wanless	JQ	Salticidae	Queensland	1, 2, 3, 4, 5	T, S, L
Bavia aericeps Simon	BA	Salticidae	Queensland	1, 4	S
Cosmophasis micarioides (L. Koch)	CO	Salticidae	Queensland	1, 4	S
Cytea sp.	CY	Salticidae	Queensland	1, 4	S
Euophrys parvula Bryant	EP	Salticidae	New Zealand	1, 4	S
Euryattus sp.	ER	Salticidae	Queensland	1, 4	S
Helpis minitabunda (L. Koch)	HM	Salticidae	Queensland	1, 4	S
Mopsus mormon Karsch	MM	Salticidae	Queensland	1, 4	S
Myrmarachne lupata L. Koch	ML	Salticidae	Queensland	1, 4	S
Plotius sp.	--	Salticidae	Queensland	4	S
Portia fimbriata	--	Salticidae	Queensland	1, 2, 3, 4, 5	T
Portia fimbriata	--	Salticidae	Northern Territory[2]	4	T
Portia labiata	--	Salticidae	Sri Lanka	4	T
Tauala lepidus Wanless	TL	Salticidae	Queensland	1, 2, 3, 4	S, L
Trite auricoma Urquhart	TA	Salticidae	New Zealand	1	S
Trite planiceps Urquhart	TP	Salticidae	New Zealand	1, 3, 4	S, L
Zenodorus orbiculatus (Keyserling)	ZO	Salticidae	Queensland	1, 4	S
Hygropoda dolomedes	HD	Pisauridae	Queensland	1, 4	S
Achaearanea krausi Chrysanthus	AC	Theridiidae	Queensland	1, 3, 4, 5	S, L

[1] All Queensland (Australia) species sympatric with P. fimbriata.

[2] Australia

were cut in half. Another petri dish of the same size was used as a test chamber (Fig. 1). A half piece of clean blotting paper was taped to one side of the inner top of the test chamber, and another half piece of clean blotting paper was aligned with the top piece and taped to the inside of the petri dish directly below ('control side'). Dragline-covered pieces of blotting paper were then taped to the inside top and inside bottom of the other half of the petri dish ('experimental side'). A triangle (each side 15-mm long), cut out of the paper, straddled the control and experimental side ('neutral area'). A horseshoe-shaped metal divider that straddled the neutral area prevented the test spider from seeing that the source spider was not present (see Clark & Jackson, 1994a).

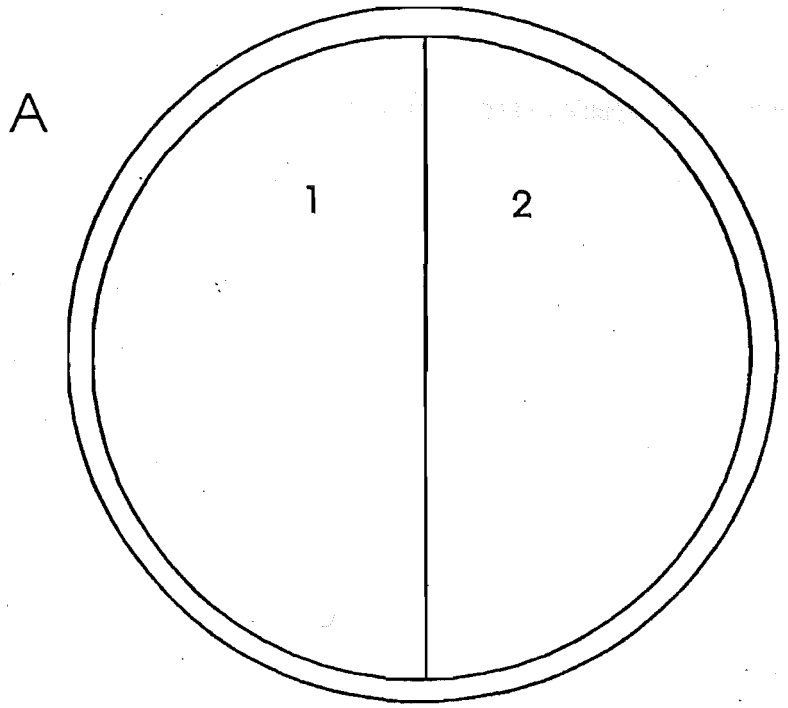
The test spider was introduced into the neutral area. Each test lasted 10 min and began when the test spider walked onto one of the pieces of blotting paper. To ascertain whether chemical cues were responsible for a spider's reactions, testing was repeated using draglines treated in one of two ways (washed in 80% ethanol or aged for 1 week). These two treatments for inactivating chemical cues have been used successfully in numerous earlier studies on salticid pheromones (see Jackson, 1987; Pollard et al., 1987).

Results

When tested with fresh draglines of J. queenslandicus, P. fimbriata spent more time on experimental than on control paper ($P<0.01$, Wilcoxon test for paired comparisons, Fig. 2a). There was no statistical evidence that draglines from any other species tested influenced the side of the chamber chosen by P. fimbriata (Fig 2d – q), nor was there statistical evidence that draglines from P. fimbriata influenced the side of the chamber chosen by J. queenslandicus's (Fig. 3). There was no statistical evidence that aged or washed draglines of J. queenslandicus influenced how P. fimbriata distributed its time on the two sides of the chamber (Fig. 2b & c).

Fig. 1. Apparatus made from petri dish used for experiment 1 (dragline choice). Two halves of dragline-covered blotting paper, one on top and one aligned on bottom of side 1. Clean blotting paper on top and bottom of side 2. A: top of dish. B: bottom of dish. D: horseshoe- shaped metal divider. N: neutral area.

Top of petri dish



Bottom of petri dish

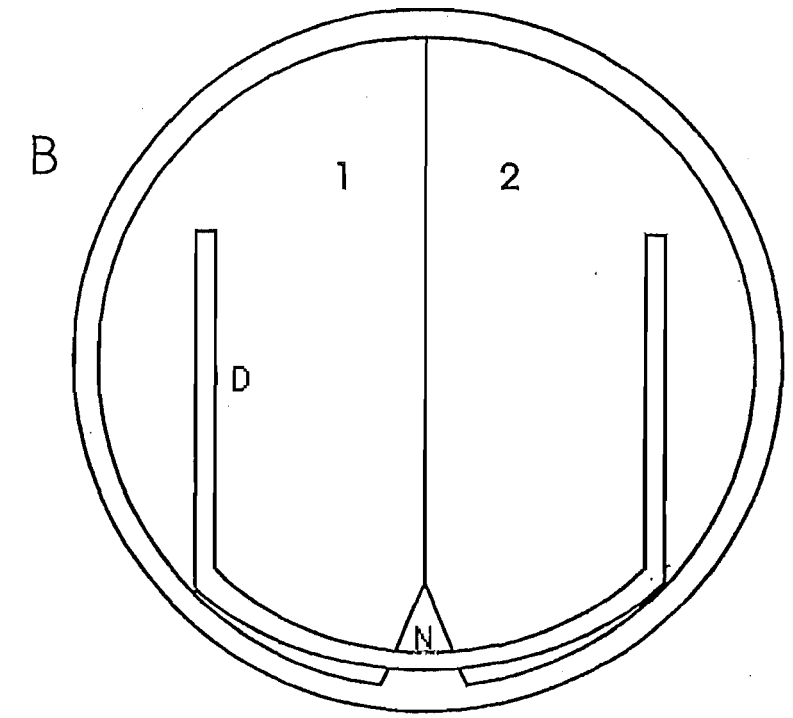
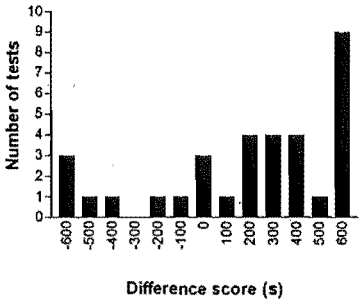
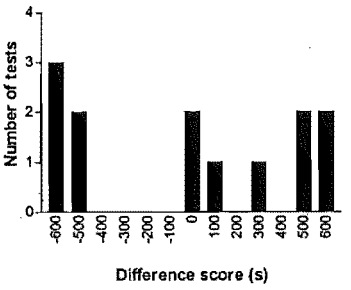


Fig. 2. Data from testing P. fimbriata in experiment 1 (dragline choice, see text). Difference score: time P. fimbriata spent on dragline-covered blotting paper (untreated draglines unless stated otherwise) minus time P. fimbriata spent on clean blotting paper. Unless stated otherwise, all species used were salticids. P. fimbriata spent significantly more time on untreated draglines from J. queenslandicus than on clean blotting paper. There was no evidence that P. fimbriata discriminated between dragline-covered and clean blotting paper in any other test.

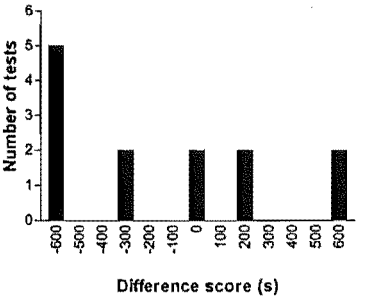
(a) Jacksonoides queenslandicus
untreated draglines
N=33



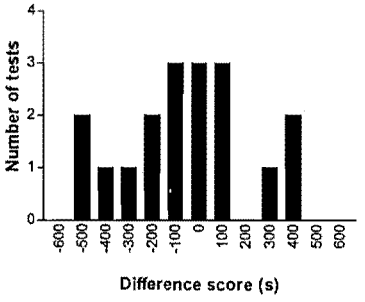
(b) Jacksonoides queenslandicus
aged draglines
N=13



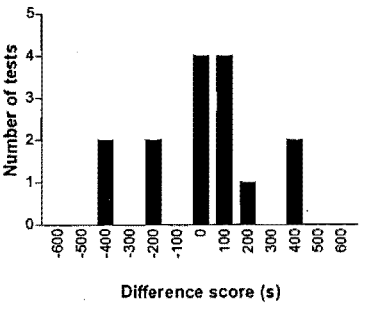
(c) Jacksonoides queenslandicus
washed draglines
N=13



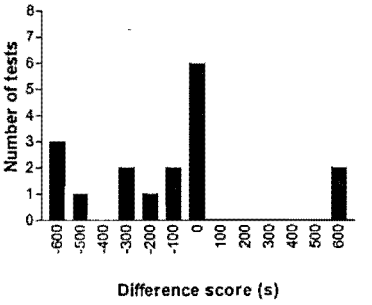
(d) Bavia aericeps
N=18



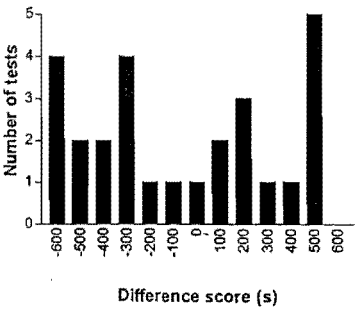
(e) Cosmophasis micariodes
N=15



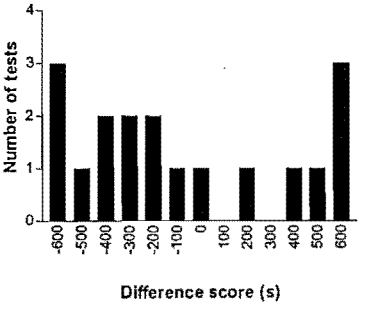
(f) Cytea sp.
N=17



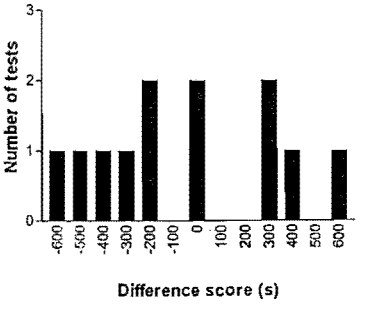
(g) Euophrys parvula
N=28



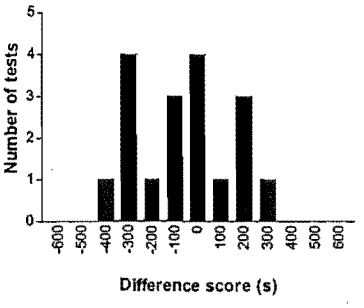
(h) Euryattus sp.
N=18



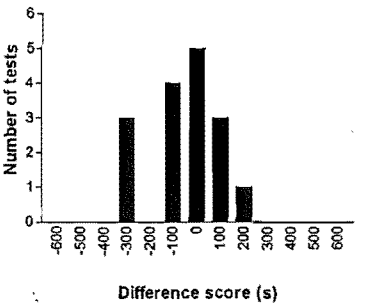
(i) Helpis minitabunda
N=12



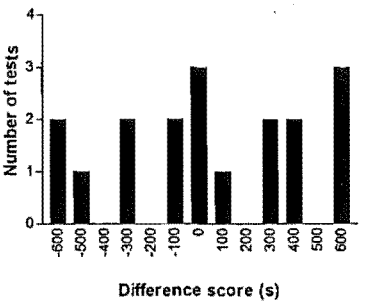
(j) Mopsus mormon
N=18



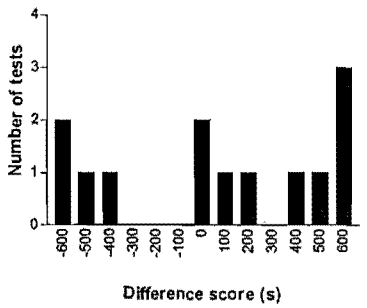
(k) Myrmarachne lupata
N=16



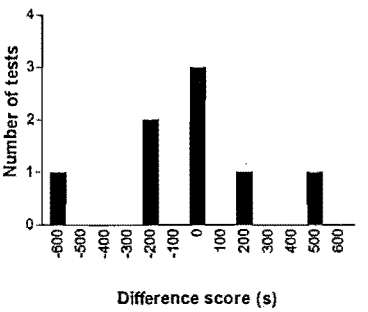
(l) Tauala lepidus
N=18



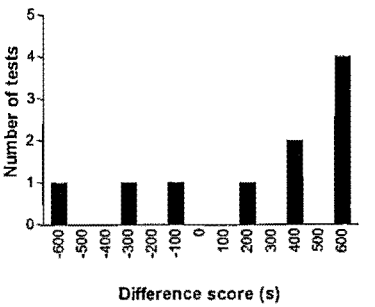
(m) Trite auricoma
N=13



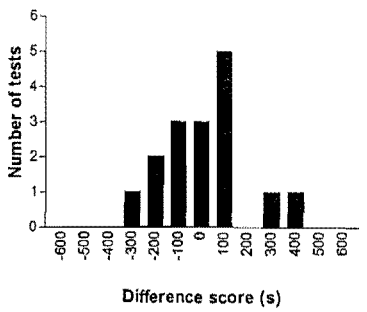
(n) Trite planiceps
N=8



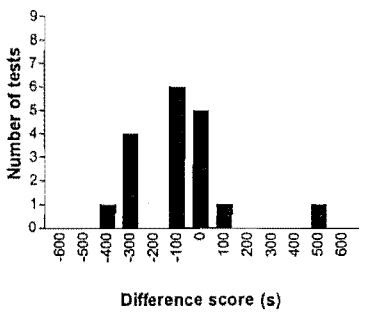
(o) Zenodorus orbiculatus
N=10



(p) Achaearanea krausi
(Theridiidae)
N=16



(q) Hygropoda dolomedes
(Pisauridae)
N=18



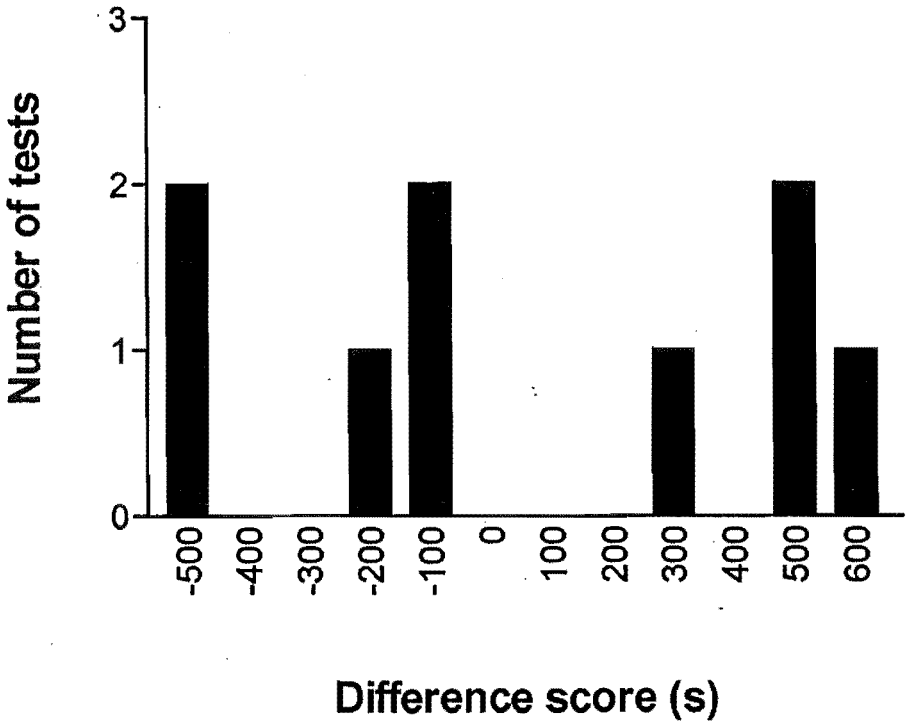


Fig. 3. Data from testing J. queenslandicus in experiment 1 (dragline choice, see text). Difference score: time J. queenslandicus spent on blotting paper covered with P. fimbriata draglines minus time J. queenslandicus spent on clean blotting paper. No statistical evidence that J. queenslandicus discriminated between blotting paper covered with P. fimbriata draglines and clean blotting paper.

EXPERIMENT 2. EFFECTS OF DRAGLINES ON BEHAVIOUR AND POSTURE

Methods

In the simple chamber used for testing dragline discrimination by P. fimbriata, no postural changes were evident. Another experiment evaluated whether, in a more natural and complex environment, posture is influenced by chemical cues from J. queenslandicus. By repeating these tests with draglines from another salticid, Tauala lepidus, we clarify whether it is cues coming specifically from J. queenslandicus that influence P. fimbriata.

The test chamber was a plastic cage (length 211 mm, width 144 mm, height 44 mm). Dry twigs and leaves were evenly spaced over the bottom surface of the chamber, covering c 30% of the area. Prior to experimental tests, a source spider (Table 1) was left for 2 h in the cage, during which time it walked around actively laying down draglines. After the 2-h period, the source spider was removed and the test spider was introduced. A test spider was initially taken into a plastic tube (65 mm long; internal diameter 11 mm), then one end of the tube was connected to a hole in the base of the cage and the other end was kept closed. Testing began when the test spider walked, on its own accord, out of the tube and into the test chamber. Whenever a test spider failed to enter the test chamber within 5 min, the test was aborted.

Each test lasted for 15 min, during which time the test spider's behaviour was recorded in detail. Control and experimental tests were comparable, except that no source spider had occupied the test chamber during the pre-test interval. Each test spider was used twice: experimental test on one day and control test on preceding or succeeding day (decided at random). Two sets of test spiders (P. fimbriata) were used, one with J. queenslandicus and one with T. lepidus used as source spiders (18 test pairs for each species of source spider).

Results

Test spiders never retracted their palps in experimental tests with T. lepidus draglines, nor any of the control tests. However, six test spiders retracted their palps in experimental tests with J. queenslandicus draglines (McNemar test for significance of changes, $P<0.05$).

EXPERIMENT 3. EFFECT OF DRAGLINES ON ATTENTION TO OPTICAL CUES

Methods

When we considered in experiments 1 and 2 how P. fimbriata responded to substrates over which J. queenslandicus had walked, no prey were in the test arena. Here, using motionless lures, we investigate whether draglines from prey influence how quickly P. fimbriata locates prey.

Except for details described below, the test chamber and procedure were as in experiment 2. Testing did not follow a paired design. In each test, a lure was present, always centred 40 mm from one end of the cage and oriented so that it faced the lower end of the cage. The test chamber (Fig. 4) was inclined at 20°, with the lure at the raised end. Testing started when a spider entered at the lower end. Test spiders tended to walk upward in the chamber, thereby getting closer to the lure.

We recorded the latency for test spiders to begin stalking (turned toward lure and walked more or less directly toward it) and to get close (within 15 mm) to lures. Test spiders never came within 15 mm of lures unless they were stalking. Tests ended when P. fimbriata got close or after 1 h elapsed, after which spiders were removed.

Four species were used for making lures and the same four species were also used as source spiders (Table 1). Spiders used for lures were first immobilised under carbon dioxide, then

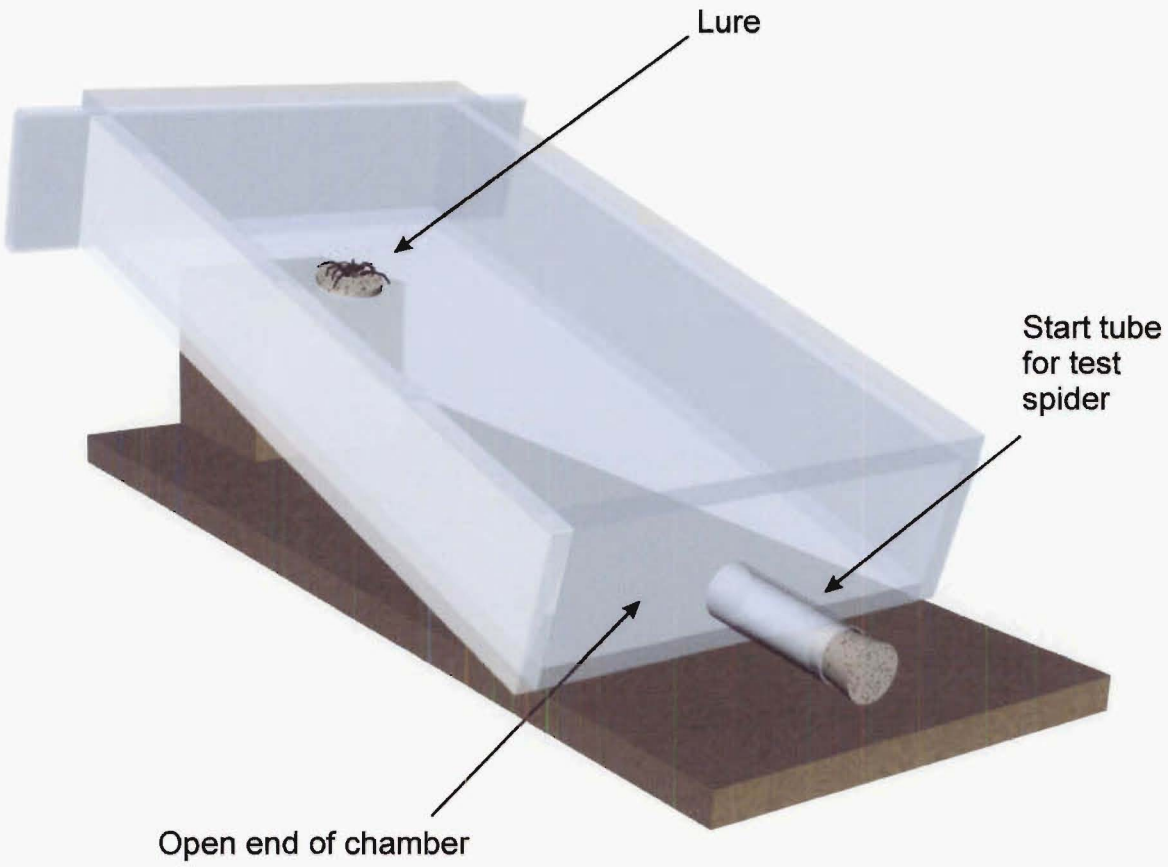


Fig. 4. Apparatus for presenting lures during experiment 3 (effects of draglines on P. fimbriata's attention to optical cues from lures). Rectangular cage (211 mm length X 144 mm width X 44 mm depth), covered by rectangular piece of glass (same as cage). Cage inclined at c. 20°. Test spider enters cage via plastic tube at lower end of cage. Lure (centred 40 mm from higher end) oriented so that it faces test spider at beginning of test.

preserved in 80% ethanol. A lure was made by removing the spider, letting it dry, then mounting it centred on a disc-shaped piece of cork (diameter c 1.25 X spider's body length). The mounted dead spider and the cork were sprayed with an aerosol plastic adhesive (Crystal Clear Lacquer, Atsco Australia Pty) for preservation and to mask chemical traces that might have remained on the dead spider.

There were four control tests (no source spider), one with each species used as a lure. There were four experimental tests in which J. queenslandicus was the source spider, one with a J. queenslandicus lure and three in which another species was used as the lure. There were another two experimental tests in which the lure was J. queenslandicus and another species was the source spider. There were three tests in each of which one of the other three test species was used as both the source spider and the lure.

As the sample size in two treatments (J. queenslandicus lure in cages with Tauala lepidus or Trite planiceps draglines) was low, we merged these treatments for the purpose of statistical analysis. Data from these two treatments are not significantly different.

Results

During testing, not all spiders began to stalk lures (Table 2), and some of those that did stalk lures failed to get close (Table 3). Tests in which stalking or getting close did not occur are not included in statistical analysis of latencies for initiation of stalking and getting close.

The latency to begin stalking J. queenslandicus lures was influenced by the type of dragline in cages (Kruskal-Wallis test, $N=29$, $P<0.05$; Fig. 5, a – c). Pairwise comparisons show that test spiders began to stalk J. queenslandicus lures in cages with J. queenslandicus draglines sooner than when in cages with no draglines (Mann-Whitney test with Bonferroni adjustment, $N=22$, $P<0.05$; compare a & b in Fig. 5) or in cages with draglines from another salticid (either Tauala

Table 2. Number of times Portia fimbriata stalked lures during experiment 3 (effect of contact cues on attention to optical cues).

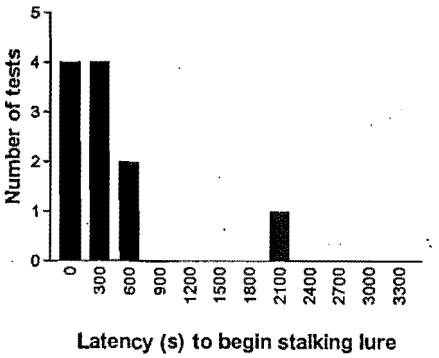
Type of lure	Dragline source	Stalked lure	Did not stalk lure
Achaearanea krausi	none	2	5
Jacksonoides queenslandicus	none	11	2
Tauala lepidus	none	5	5
Trite planiceps	none	3	6
Achaearanea krausi	Jacksonoides queenslandicus	4	4
Jacksonoides queenslandicus	Jacksonoides queenslandicus	11	2
Tauala lepidus	Jacksonoides queenslandicus	4	10
Trite planiceps	Jacksonoides queenslandicus	2	7
Achaearanea krausi	Achaearanea krausi	3	6
Jacksonoides queenslandicus	Tauala lepidus or Trite planiceps	7	13
Tauala lepidus	Tauala lepidus	7	5
Trite planiceps	Trite planiceps	5	7

Table 3. Number of times Portia fimbriata got close (within 15 mm) to lures during experiment 3 (effect of contact cues on attention to optical cues).

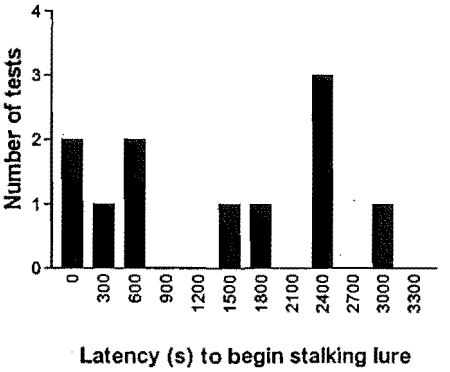
Type of lure	Dragline source	Got close to lure	Did not get close to lure
Achaearanea krausi	none	2	5
Jacksonoides queenslandicus	none	3	10
Tauala lepidus	none	4	6
Trite planiceps	none	2	7
Achaearanea krausi	Jacksonoides queenslandicus	3	5
Jacksonoides queenslandicus	Jacksonoides queenslandicus	5	8
Tauala lepidus	Jacksonoides queenslandicus	1	13
Trite planiceps	Jacksonoides queenslandicus	0	9
Achaearanea krausi	Achaearanea krausi	1	5
Jacksonoides queenslandicus	Tauala lepidus or Trite planiceps	2	18
Tauala lepidus	Tauala lepidus	6	6
Trite planiceps	Trite planiceps	4	8

Fig. 5. Data from experiment 3 (effect of draglines on attention, see text). Latency (s) for P. fimbriata to begin stalking lures while on draglines.

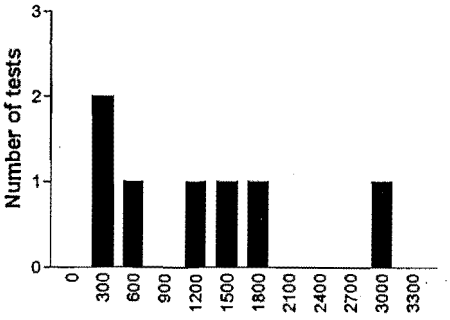
(a) Lure made from Jacksonoides queenslandicus
Draglines of Jacksonoides queenslandicus



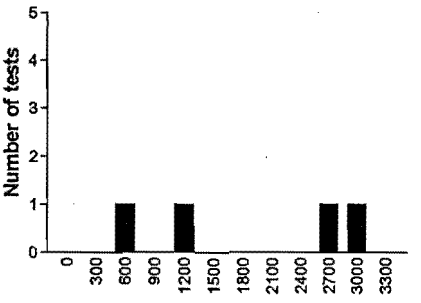
(b) Lure made from Jacksonoides queenslandicus
No draglines



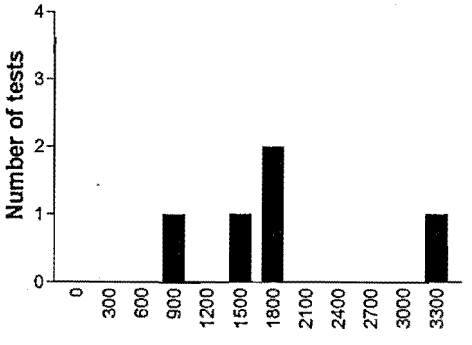
(c) Lure made from Jacksonoides queenslandicus
Draglines of Tauala lepidus or Trite planiceps



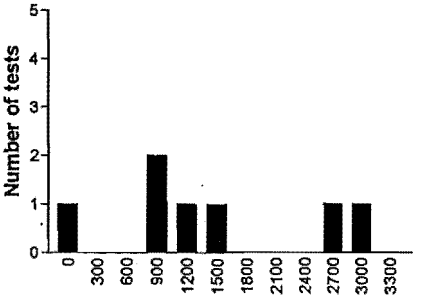
(d) Lure made from Tauala lepidus
Draglines of Jacksonoides queenslandicus



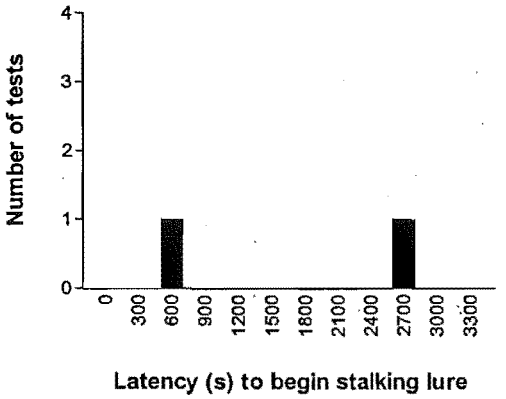
(e) Lure made from Tauala lepidus
No draglines



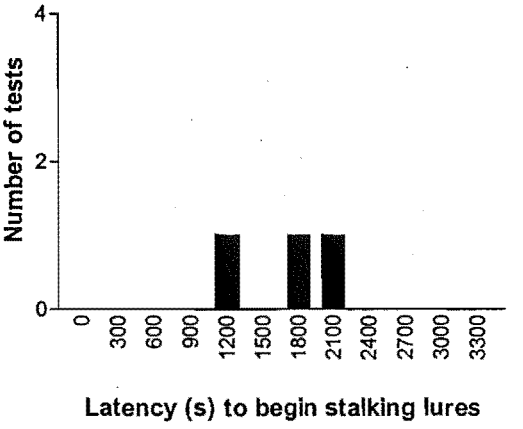
(f) Lure made from Tauala lepidus
Draglines of Tauala lepidus



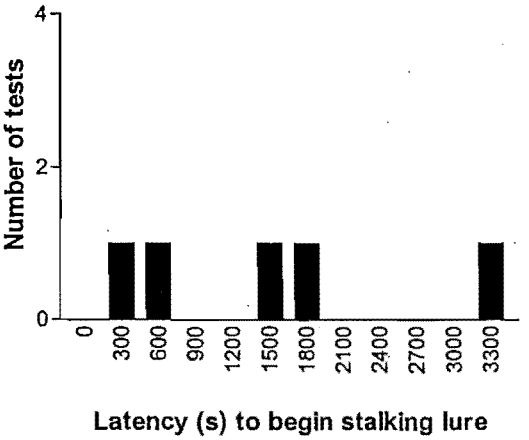
(g) Lure made from Trite planiceps
Draglines of Jacksonoides queenslandicus



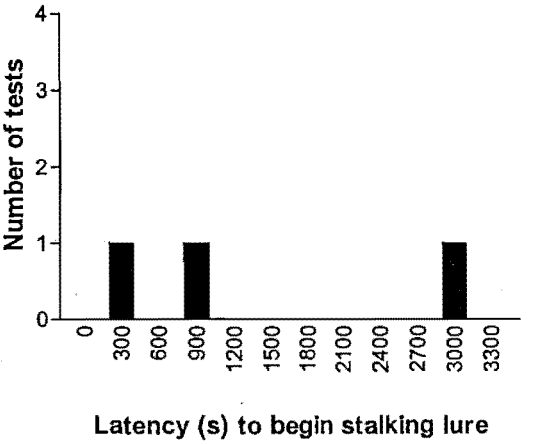
(h) Lure made from Trite planiceps
No draglines



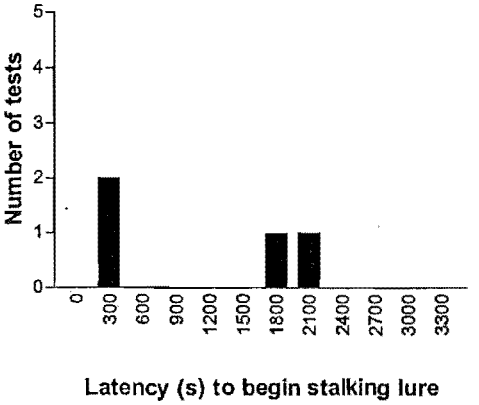
(i) Lure made from Trite planiceps
Draglines of Trite planiceps



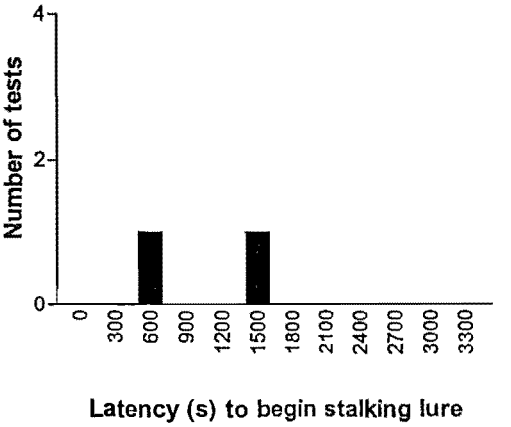
(j) Lure made Achaearanea krausi
Draglines of Achaearanea krausi



(k) Lure made from Achaearanea krausi
Draglines of Jacksonoides queenslandicus



(l) Lure made from Achaearanea krausi
No draglines



lepidus or Trite planiceps) (Mann-Whitney test with Bonferroni adjustment, N=18, P<0.05; compare a & c). There was no statistical evidence that type of dragline influenced the latency to begin stalking lures made from Tauala lepidus (Kruskal-Wallis test, N=16, P=0.748; compare d – f), Trite planiceps (Kruskal-Wallis test, N=10, P=0.802; compare g – i) or Achaearanea krausi (Kruskal-Wallis test, N=9, P=0.962; compare j – l).

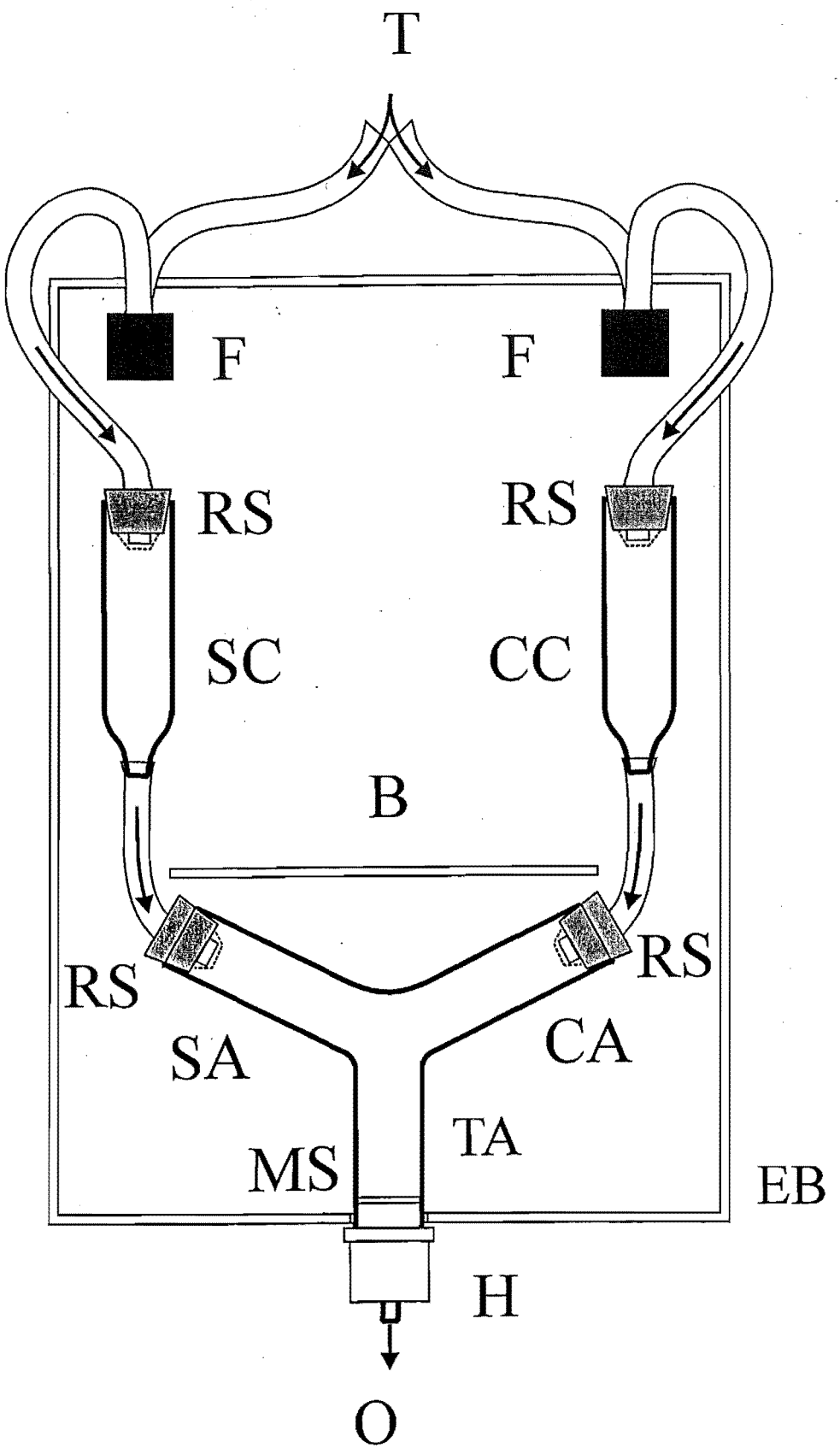
There was no statistical evidence that type of dragline influenced the latency to get close to lures made from J. queenslandicus (Kruskal-Wallis test, N=11, P=0.493) (J. queenslandicus lure on Tauala lepidus draglines not included in this analysis, as test spiders never got close to lures in these tests). Nor was there statistical evidence that type of dragline influenced the latency to get close to lures of Tauala lepidus (Kruskal-Wallis test, N=10, P=0.564) or A. krausi (Kruskal-Wallis test, N=7, P=0.325). No test spiders got close to Trite planiceps lures in cages with Trite planiceps draglines, nor was there statistical evidence that the latency to get close to Trite planiceps lures was influenced by draglines from J. queenslandicus (Mann-Whitney test, N=5, P=0.600).

EXPERIMENT 4. OLFACTOMETER TESTS

Methods

A Y-shaped olfactometer (Fig. 6) with airflow adjusted to 1500 ml/min (Matheson FM-1000 flowmeter) was used to assess P. fimbriata's response to airborne odours from prey. At this airflow setting, there was no evidence that P. fimbriata's locomotion was impaired. Air moved from a tap through two separate flowmeters into two chambers: a stimulus chamber (contained odour source) and control chamber (empty). Whether the stimulus chamber was on the left or right side of the olfactometer was decided at random. Air moved from the stimulus chamber to the stimulus arm,

Fig. 6. Olfactometer. Arrows indicate direction of airflow. SC: stimulus chamber (contains source spider). CC: control chamber (empty). Dimensions of both SC and CC: 115 mm length, 25 mm internal diameter. H: holding chamber (location of test spider at start of test; length 40 mm, internal diameter 20 mm). RS: rubber stopper. TA: test arm. CA: control arm. SA: stimulus arm. Dimensions of TA, CA and SA; length 90 mm, internal diameter 20 mm. MS: metal screen fitted in slit (blocks test spider's entry into test arm before test begins). T: tap from which air enters olfactometer. F: flowmeter. B: opaque barrier (prevents test spider from seeing source spider). O: opening for air to leave olfactometer. EB: external box (minimises disturbances to test spider caused by movement outside the test apparatus). Diagram not to scale. See text for details.


T
F
F
RS
RS
SC
CC
B
RS
RS
SA
CA
TA
MS
EB
H
O

and independently from the control chamber to the control arm (collectively, the two are referred to as the "choice arms"). Air moved from the two choice arms and mixed as it entered the stem of the 'Y'. At the end of the stem, furthest from the choice arms, there was a holding chamber into which a spider was placed before testing. A metal barrier, positioned in a slit between the holding chamber and the stem, blocked the spider's entry into the test arm. An odour source was placed in the stimulus chamber 30 min before each test. The 30-min period allowed air to circulate evenly and ensured that air pressure was comparable throughout the olfactometer.

During testing, spiders tended to walk about actively in the olfactometer, sometimes making brief entries (< 30 s) into the stimulus or control arm, or both. By definition, the spider made its choice when it entered a choice arm and remained for 30 s. After leaving the holding chamber, the spider was allowed 1 h to make a choice. We recorded the arm chosen and the latency to choose that arm. As a precaution against traces from previously tested spiders, the olfactometer was dismantled and cleaned with ethanol followed by water, between tests.

Results

When J. queenslandicus was the odour source in the stimulus chamber, Queensland P. fimbriata's choice was the stimulus arm more often than the control arm (16 chose the stimulus arm, 3 chose the control arm; binomial test of independence, $P<0.001$). When other spider species were used as odour sources, there was no evidence that Queensland P. fimbriata distinguished between the stimulus and control arms (Table 4), nor was there statistical evidence that the latency to choose between the stimulus and control arms depended on the species used for the odour source (Fig. 7). No statistical evidence was found that P. fimbriata from the Northern Territory or P. labiata from the Philippines discriminated between J. queenslandicus odour and clean air (Table 4).

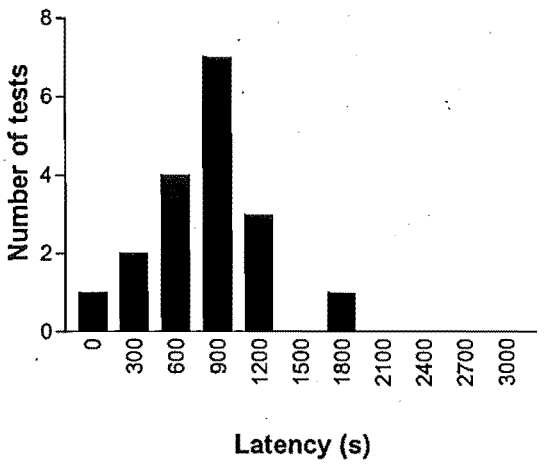
Table 4. Olfactometer arm chosen by three types of Portia during experiment 4. See Fig. 6 and text.

Test spider	Source species	N	Chose stimulus arm	Chose control arm	Binomial test[1]
Queensland Portia fimbriata	Jacksonoides queenslandicus	19	16	3	P<0.001
Northern Territory Portia fimbriata	Jacksonoides queenslandicus	17	10	7	NS
Sri Lankan Portia labiata	Jacksonoides queenslandicus	18	8	10	NS
Queensland Portia fimbriata	Achaearanea krausi	18	7	11	NS
Queensland Portia fimbriata	Bavia aericeps	17	7	10	NS
Queensland Portia fimbriata	Cosmophasis micaroides	16	6	10	NS
Queensland Portia fimbriata	Cytea sp.	20	10	10	NS
Queensland Portia fimbriata	Euophrys parvula	16	9	7	NS
Queensland Portia fimbriata	Euryattus sp.	20	12	8	NS
Queensland Portia fimbriata	Helpis minitabunda	17	8	9	NS
Queensland Portia fimbriata	Hygropoda dolomedes	18	10	8	NS
Queensland Portia fimbriata	Mopsus mormon	16	9	7	NS
Queensland Portia fimbriata	Myrmarachne lupata	17	7	10	NS
Queensland Portia fimbriata	Plotius sp.	17	7	10	NS
Queensland Portia fimbriata	Tauala lepidus	20	11	9	NS
Queensland Portia fimbriata	Trite planiceps	18	10	8	NS
Queensland Portia fimbriata	Zenodorus orbiculatus	17	9	8	NS

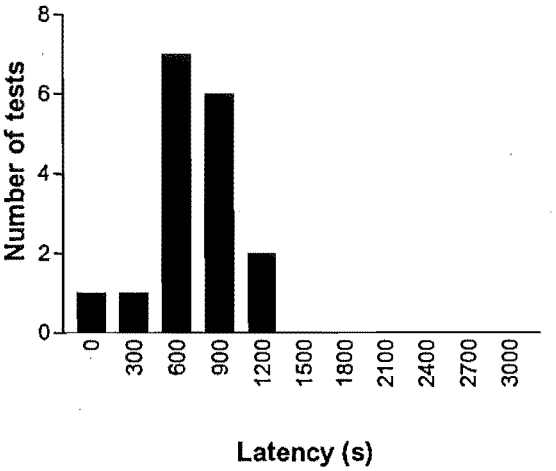
[1] Null hypothesis: probability of choosing same as probability of choosing the control arm

Fig. 7. Data from experiment using olfactometer. Latency (median in s) for Queensland P. fimbriata to make choice between experimental and control arm of olfactometer. Number of tests with each species used as odour source: Achaearanea krausi, 18; Bavia aericeps, 17; Cosmophasis micarioides, 16; Cytea sp., 20; Euophrys parvula, 16; Euryattus sp., 20; Helpis minitibunda, 17; Hygropoda dolomedes, 18; Jacksonoides queenslandicus, 19; Myrmarachne lupata, 17; Mopsus mormon, 16; Plotius sp., 17; Tauala lepidus, 20; Trite planiceps, 18; Zenodorus orbiculatus, 17. Unless stated otherwise, all species used are salticids. Note: Kruskal-Wallis test provided no statistical evidence that latencies differed.

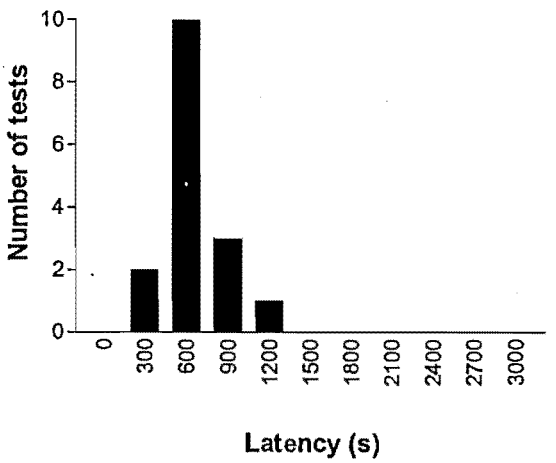
(a) Achaearanea krausi
N=18



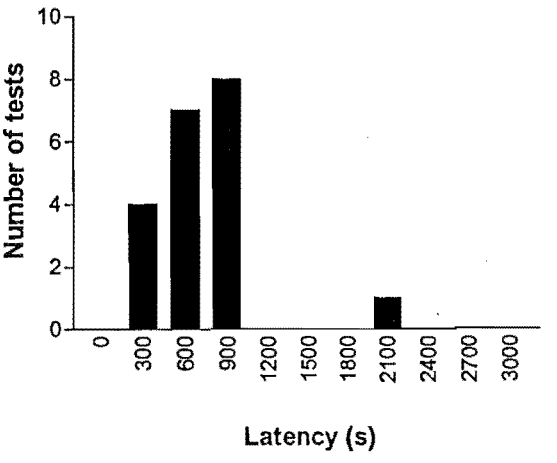
(b) Bavia aericeps
N=17



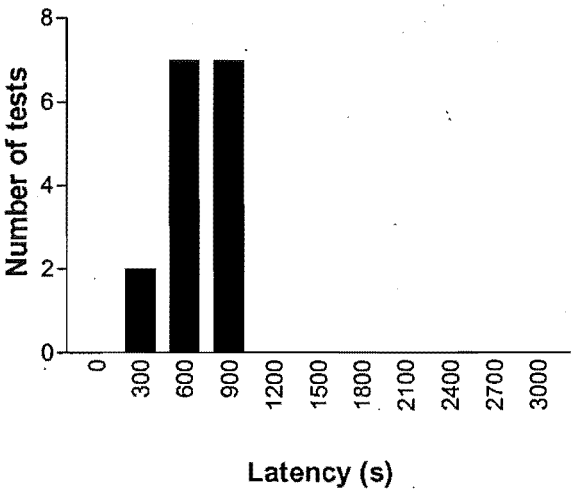
(c) Cosmophasis micariodes
N=16



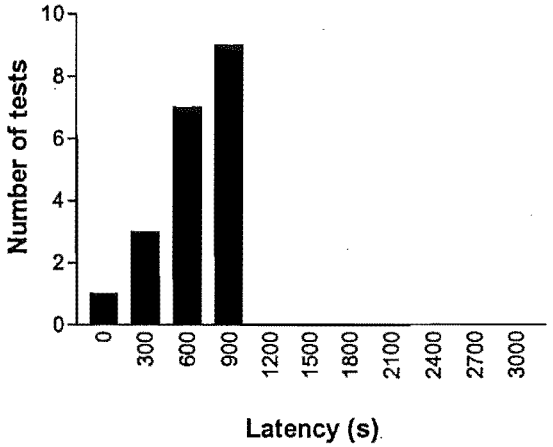
(d) Cytea sp.
N=20



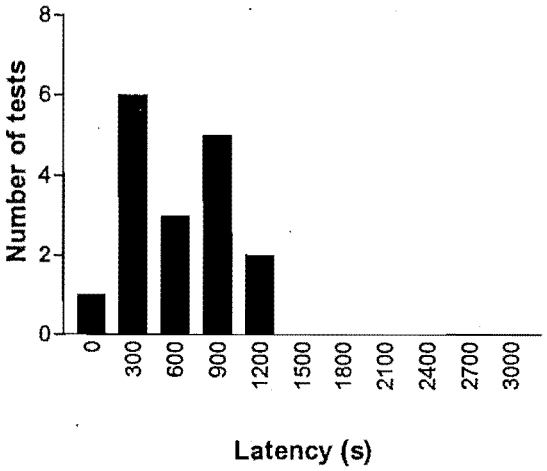
(e) Euophrys parvula
N=16



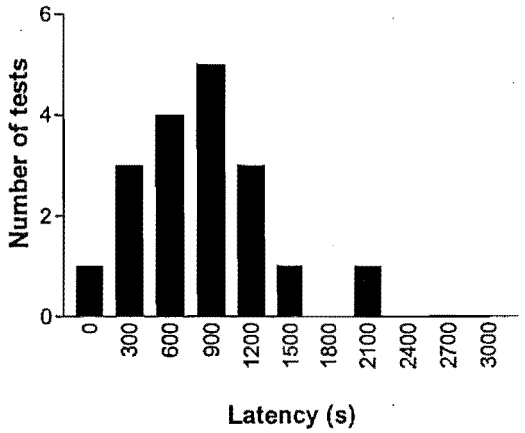
(f) Euryattus sp.
N=20



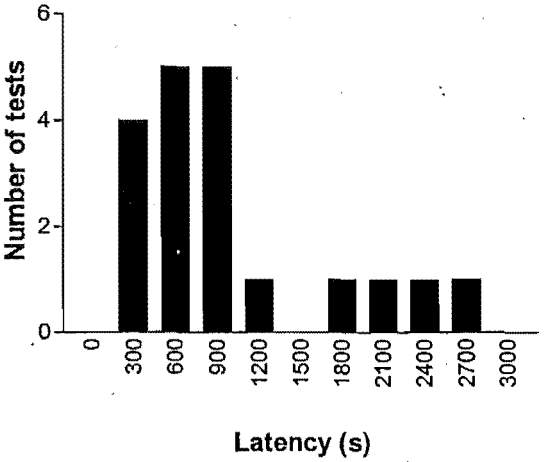
(g) Helpis minitibunda
N=17



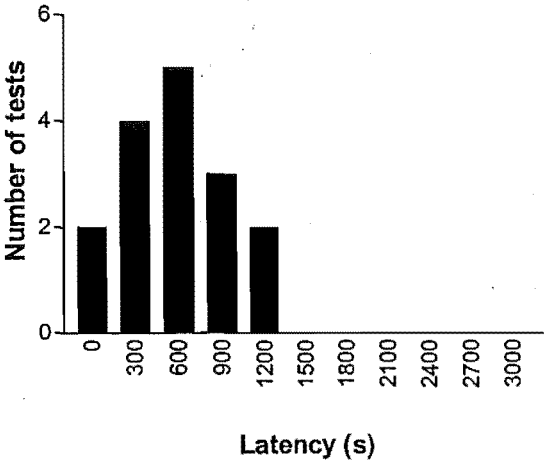
(h) Hygropoda dolomedes
(Pisauridae)
N=18



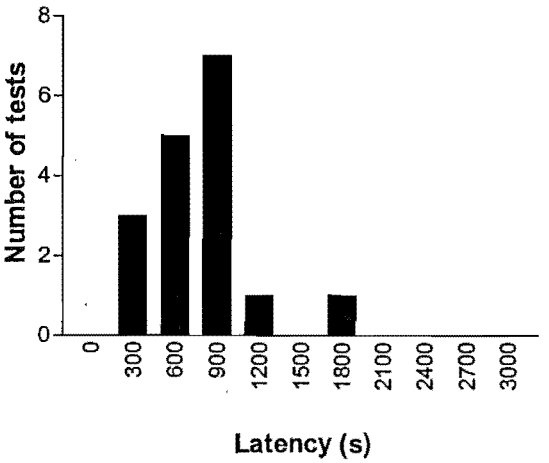
(i) Jacksonoides queenslandica
N=19



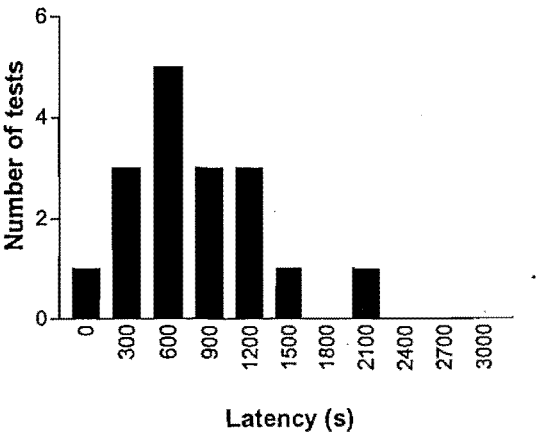
(j) Mopsus mormon
N=16



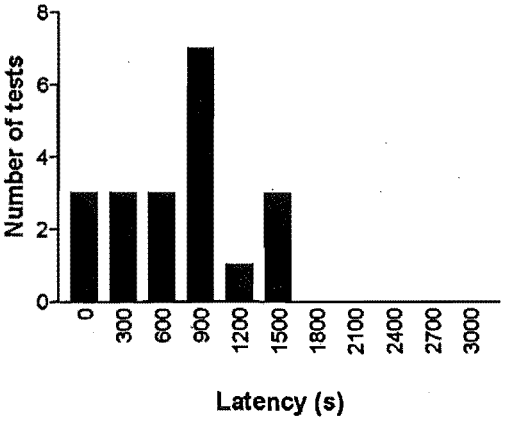
(k) Myrmarachne lupata
N=17



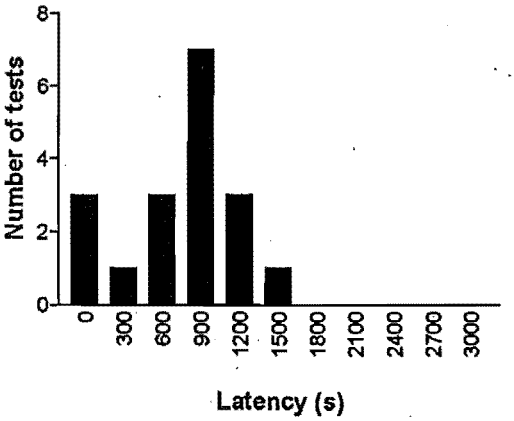
(l) Plotius sp.
N=17



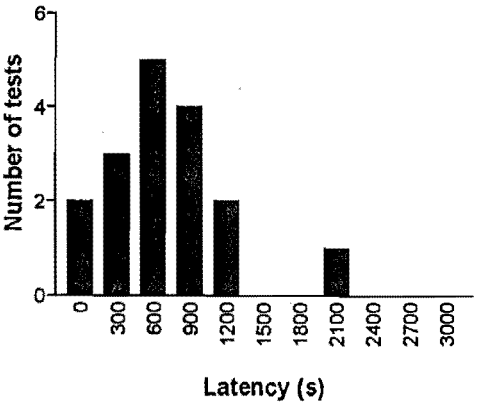
(m) Tauala lepidus
N=20



(n) Trite planiceps
N=18



(o) Zenodonus orbiculatus
N=17



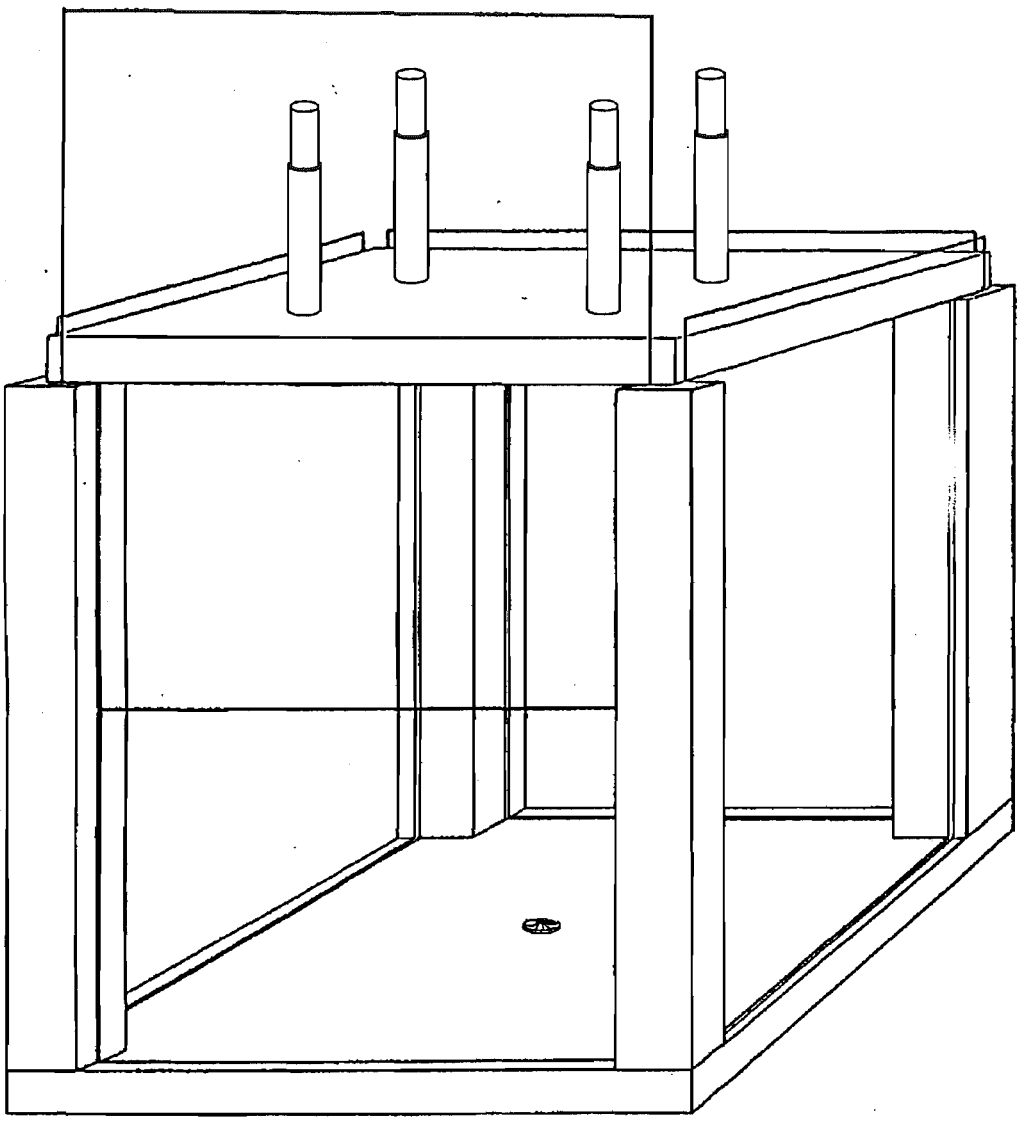
EXPERIMENT 5. EFFECT OF OLFACTORY CUES ON ATTENTION TO OPTICAL CUES

Methods

The test chamber (Fig. 8) was a wooden frame cage (200 mm square) with removable glass sides. A P. fimbriata was put into the cage 5-7 days prior to testing (during which time no prey was provided) and allowed to make a web. During experiments, odour was introduced to the test chamber via four plastic tubes, one attached to each of the four holes in the top of the cage. A small screen-covered vial was attached to the distal end of each tube, and a spider (odour source) was placed in each vial.

An odour source was a spider in a vial. Either, four odour sources (same spider species) or four empty control vials were first placed in the tubes and connected to the cage, then testing begun 60 min later by inserting a lure through the hole in the bottom of the cage. Testing was aborted if the test spider was out of its web at the 60-min interval. Lures on corks were made as described earlier (see experiment 3). To introduce the lure, the cork was inserted through the hole in the bottom of the cage. Definitions of behaviour were as described earlier, but an additional behaviour, dropping on draglines, was relevant to this experiment: P. fimbriata attached dragline to the web, then dropped down toward the lure, making intermittent brief pauses along the way (see Chapter 4). Control and experimental tests were the same, except there were no source spiders in controls. Each test spider was used twice: experimental test on one day and control test on preceding or succeeding day (decided at random). A separate set of tests was carried out using J. queenslandicus as lure and source spider, A. krausi as lure and source spider, J. queenslandicus as lure and A. krausi as source spider, and A. krausi as lure and J. queenslandicus as source spider.

Fig. 8. Cage used in experiment 5. Wooden frame (200 mm x 200 mm x 200 mm interior dimensions), with five cork holes (diameter 13 mm), and four removable glass sides. Top and bottom are wooden. Glass fits in grooves in frame (front glass shown partly raised). Four holes at top (spaced in a square) for introducing prey during normal maintenance feeding. During experimental tests, plastic tube connected to each hole in top. A source spider in screen-covered vial connected to other end of tube. Tubes connected 60 min prior to start of test. Hole in bottom of cage (centred) for presentation of lure. Glass sides can be lifted (as in drawing).



Results

P. fimbriata dropped on draglines towards J. queenslandicus lures more often when in cages with J. queenslandicus odour than when in cages with no odour (Table 5), but there was no statistical evidence that P. fimbriata's tendency to drop on draglines towards J. queenslandicus lures was influenced by A. krausi odours. Nor was there any statistical evidence that P. fimbriata's tendency to drop on draglines towards A. krausi lures was influenced by odours from either J. queenslandicus or A. krausi.

There was no statistical evidence that P. fimbriata's tendency to retract its palps, in response to either J. queenslandicus or A. krausi lures, was influenced by odours from either J. queenslandicus or A. krausi (Table 6).

P. fimbriata's latency to get close to J. queenslandicus lures was significantly shorter when in the presence of J. queenslandicus odour than when in cages where no odour was present (Table 7). In contrast, there was no statistical evidence that J. queenslandicus odour affected the latency for P. fimbriata to get close to A. krausi lures, nor was there statistical evidence that A. krausi odours affected P. fimbriata's response to either type of lure.

DISCUSSION

In experiment 1 (dragline-choice tests) P. fimbriata stayed longer on blotting paper where J. queenslandicus draglines were present rather than on clean blotting paper. This experiment was repeated using procedures (washing silk in ethanol or ageing for one week) known from previous studies (Jackson, 1987; Pollard et al., 1987) to inactivate chemical cues on dragline, nest and web silk. After these treatments, there was no evidence that P. fimbriata discriminated between blotting

Table 5. Tendency of Portia fimbriata to drop on draglines toward lure during experiment 5: each P. fimbriata tested on one day with odour present (experimental test) and on alternate day (previous or next, decided at random) with odour absent (control). P. fimbriata more often dropped on draglines in response to Jacksonoides queenslandicus lures in cages with J. queenslandicus odours, than in control cages ($P<0.05$, McNemar test for significance of changes).

Source spider used for odours	Spider used for lure	Dropped on draglines in experimental test only	Dropped on dragline draglines in control test only	Dropped on draglines in both tests	Dropped on draglines in neither test
Jacksonoides queenslandicus	Jacksonoides queenslandicus	4	0	2	12
Jacksonoides queenslandicus	Achaearanea krausi	1	2	0	15
Achaearanea krausi	Achaearanea krausi	1	0	1	16
Achaearanea krausi	Jacksonoides queenslandicus	0	1	1	16

Table 6. Tendency of Portia fimbriata to retract palps during experiment 5: each P. fimbriata tested on one day with odour present (experimental test) and on alternate day (previous or next, decided at random) with odour absent (control). No statistical evidence that presence of odours affected tendency of P. fimbriata to retract palps in response to lures.

Source spider used for odours	Spider used for lures	Retracted palps in experimental test only	Retracted palps in control test only	Retracted palps in both tests	Retracted palps in neither test
Jacksonoides queenslandicus	Jacksonoides queenslandicus	5	2	3	8
Jacksonoides queenslandicus	Achaearanea krausi	0	0	0	18
Achaearanea krausi	Achaearanea krausi	0	0	0	18
Achaearanea krausi	Jacksonoides queenslandicus	5	3	3	7

Table 7. Latency for Portia fimbriata to get close to lures during experiment 5: each P. fimbriata tested on one day with no odour present (control) and on alternate day with odours from a sympatric prey species (experimental). P. fimbriata got closer to J. queenslandicus lures significantly sooner in cages with Jacksonoides queenslandicus odours (Wilcoxon-signed rank test, $P<0.01$), than when in control cages. However, there was no evidence that J. queenslandicus odours affected the latency to get close to Achaearanea krausi lures, or that A. krausi odours affected the latency to get close to either lures made from A. krausi or J. queenslandicus.

Odour source spider	Type of lure	Test	N[1]	First Quartile	Median	Third Quartile
Achaearanea krausi	Achaearanea krausi	no odour	3	1181	2073	2916
Achaearanea krausi	Achaearanea krausi	odour	3	1971	2350	3090
Achaearanea krausi	Jacksonoides queenslandicus	no odour	3	1224	1779	2643
Achaearanea krausi	Jacksonoides queenslandicus	odour	3	1964	2106	2502
Jacksonoides queenslandicus	Achaearanea krausi	no odour	5	1203	1947	2841
Jacksonoides queenslandicus	Achaearanea krausi	odour	5	1240	2333	3092
Jacksonoides queenslandicus	Jacksonoides queenslandicus	no odour	7	1820	2307	2483
Jacksonoides queenslandicus	Jacksonoides queenslandicus	odour	7	526	975	1738

[1] Number of pairs of tests (tests in cages with odour present or absent). Data from test pairs excluded whenever test spiders failed to get close to lures in both the experimental and control tests.

paper coated with silk from J. queenslandicus and clean blotting paper, supporting the hypothesis that the relevant cue is chemical.

In experiment 2, contact chemical cues on draglines elicited postural changes: in the presence of draglines from J. queenslandicus, but in the absence of optical cues from J. queenslandicus, P. fimbriata often retracted its palps, palp retraction being a routine component of P. fimbriata's tactics when pursuing J. queenslandicus. Portia fimbriata tended to stay on draglines of J. queenslandicus, but there was no evidence that draglines of other species had a comparable effect. Experiment 4 showed that P. fimbriata is attracted to olfactory cues from J. queenslandicus, with P. fimbriata moving more often into an area of an olfactometer having volatile chemical cues from J. queenslandicus and less often into an area having clean air. Experiments 3 (contact cues) and 5 (olfactory cues) provide evidence that P. fimbriata's attention to location-revealing optical cues is enhanced by encounters with chemical cues from J. queenslandicus, suggesting integrated reliance on visual and chemical cues. In both of these experiments, we demonstrated responses by P. fimbriata to J. queenslandicus, but not to other prey species. This suggests that P. fimbriata's sensitivity is focused on chemical cues specifically from J. queenslandicus, rather than generally on other spiders or even other salticids.

In the natural environment, where numerous visual obstructions are present, it may be advantageous for P. fimbriata to be sensitive to both olfactory and contact chemical cues. Olfactory cues, being volatile plumes subject to rapid dissipation and diffusion by wind (Bossert & Wilson, 1963; Alberts, 1992), may be especially useful at revealing from a distance the presence and identity of prey currently in the environment. Contact cues, on the other hand, tend to be detectable over only short distances, but they usually remain in the environment for longer than olfactory cues (Wilson & Bossert, 1963), thereby being especially useful for revealing that an area is frequented by the prey.

The behaviour of five species of Portia (P. africana, P. albimana, P. fimbriata, P. labiata and P. schultzi) from a wide range of African, Asian and Australian habitats has been studied (Jackson, & Hallas 1986a), but only the Queensland P. fimbriata practises cryptic stalking. Cursorial salticids are exceptionally abundant in the Queensland habitat of P. fimbriata, but J. queenslandicus appears to be the dominant species (Jackson, 1988). Using cryptic stalking, the Queensland P. fimbriata is effective at preying on a wide range of salticid species. It is tempting to argue that cryptic stalking evolved as a tactic for capturing salticids in general. This study suggests an alternative hypothesis, that J. queenslandicus, being by far the most abundant salticid in P. fimbriata's Queensland habitat, has been the particular prey that has exerted the primary selective pressure responsible for the evolution of cryptic stalking. The usefulness of cryptic stalking for capturing salticids other than J. queenslandicus may be, to a significant degree, incidental. Not only the highly focused chemosensory system revealed by the present study, but also cryptic stalking, may have been derived by natural selection as an adaptation for capturing this one exceptionally abundant prey species.

CHAPTER 4:

WEB USE DURING PREDATORY ENCOUNTERS BETWEEN PORTIA FIMBRIATA, AN ARANEOPHAGIC JUMPING SPIDER, AND ITS PREFERRED PREY, OTHER JUMPING SPIDERS

ABSTRACT

Most salticids are cursorial spiders that prey primarily on insects, but Portia fimbriata is a web-building and web-invading araneophagic salticid. When in its own web, in the field, P. fimbriata's prey was other spiders especially Jacksonoides queenslandicus, a salticid spider that routinely enters webs of other spiders. How P. fimbriata uses its web in predatory sequences with salticid prey was investigated in the laboratory: besides using the web as a vantage point from which to initiate stalking of salticids seen near the web, P. fimbriata also dropped on draglines to attack salticids walking below the web. Salticids that enter the web are ambushed when they come close.

INTRODUCTION

Salticids have unusually complex eyes and acute vision (Land 1969a, b; Blest et al., 1990), and most species are insectivorous hunting spiders (Richman & Jackson, 1992; Jackson & Pollard, 1996). Portia is exceptional, as the species in this salticid genus are versatile predators that prefer other spiders as prey (Li et al., 1997). These remarkable salticids not only hunt away

from webs but also build prey-capture webs and make predatory raids into other spiders' webs where they may eat the resident spider's eggs, the resident spider, and ensnared insects. Spiders in alien webs are not simply stalked or chased down, but instead deceived and manipulated by aggressive mimicry signals prior to being attacked (Jackson & Wilcox, 1998).

Among previously studied species and populations of Portia, P. fimbriata (Doleschall) from Queensland is exceptional because it prefers salticids over other types of spiders (Li & Jackson, 1996a). Nesting salticids are enticed out of their nests by aggressive-mimicry signals, and a special tactic, cryptic stalking, enables the Queensland P. fimbriata to be effective at capturing salticids in the open, away from nests and webs (Jackson & Blest, 1982a; Jackson & Hallas, 1986b).

Morphologically, Portia resembles a piece of detritus (Wanless, 1978b). When walking, detritus mimicry is preserved by a slow, choppy gait unlike that of any other salticid (Jackson & Blest, 1982). At rest in a web, Portia adopts a special posture, called the 'cryptic rest posture', with legs close to the body and palps retracted back beside the chelicerae (Jackson & Blest, 1982a), thereby hiding the outlines of these appendages.

When cryptic stalking, the Queensland P.fimbriata exaggerates the slow, choppy gait of its normal locomotion, while holding its palps retracted back as in the cryptic rest posture. Sometimes salticids detect movement and turn to face the cryptically stalking P. fimbriata. P. fimbriata then freezes until the salticid once again faces away (Jackson & Blest, 1982a). While stalking any other type of spider or an insect, the Queensland P.fimbriata does not consistently retract its palps, nor does it tend to freeze when faced. Salticids do not readily recognise a cryptically stalking Queensland P.fimbriata as a predator, but often defend themselves when stalked by other species of Portia or by P.fimbriata from sites other than Queensland (Jackson &

Hallas, 1986a). Cursorial salticids are especially abundant in the habitat of Queensland P. fimbriata, and salticid-specific tactics appear to be an example of local adaptation to locally abundant prey (Jackson, 1992b).

Portia spp. may occasionally feed on insects captured in their own or alien webs, but all Portia species tested prefer spiders to insects as prey, whether in or out of webs (Li et al., 1997). When Portia does occasionally respond to insects in webs, it usually walks over and either lunges at them or, more often, simply tries to pick them up (Jackson & Hallas, 1986a). Portia's almost casual reaction to insects suggests that these are at most secondary prey, but it may be that insects in webs indirectly enhance Portia's ability to capture other spiders.

In nature, especially in the tropical habitats of Portia, webs are frequently contiguous (see Krafft, 1970, Avilés, 1997). Spiders in these complexes often pursue insects by entering neighbouring webs, including webs of other species. Webs of Portia are common in interspecific complexes, and spiders that enter Portia's web to pursue insects may in turn be pursued and captured by the resident Portia (Jackson & Blest, 1982a; Jackson & Hallas, 1986a). Occasionally, Portia will create a compound web by incorporating alien silk into its own web. Within web complexes, migration of spiders between webs tends to be frequent, and a web left vacant when its occupant is killed by Portia is usually soon filled by another spider (Jackson, unpub. data).

Here we investigate the potential role of the web in predatory sequences against the Queensland P. fimbriata's preferred prey, other genera of salticids.

MATERIALS AND METHODS

Prey records from the field

Over a period of 9 years, whenever P. fimbriata in Queensland was observed feeding in its own web, its prey were collected and identified. Here we consider only those instances where the web had clearly been built by P. fimbriata (i.e., we ignore instances of feeding in either compound webs or the webs of other spiders).

There were 61 prey records from the field (Table 1): 42 (68.9%) were salticids; 15 (24.6%) were spiders other than salticids; and four (6.5%) were insects (three noctuid moths and one crane fly (Tipulidae)).

Of the 42 salticid prey, 29 (69%) were Jacksonoides queenslandicus Wanless. Another eight species, including Helpis minitabunda (L. Koch) (see below), each accounted for 2-7% of the salticid prey.

Of the 15 non-salticid spiders, 12 (80%) were web-building species (families Araneidae, Pholcidae, Pisauridae & Uloboridae). The other three were clubionid, lamponid and mimetid species that are known to enter other spiders' webs and prey on the resident (Jackson & Whitehouse, 1996; Jackson, unpubl.).

Testing in the laboratory

Standard maintenance and terminology were adopted, as detailed elsewhere (Jackson & Hallas, 1986a). Testing took place in a controlled-environment laboratory (light: dark cycle, 12L:12D; lights came on at 0800 h). All test and prey spiders were adult females without eggs, and were used in only one test. All spiders came from laboratory cultures established by breeding

Table 1. Prey records of Queensland Portia fimbriata in own web in nature

Order	Family	Species	Description	No. of records
Araneae	Salticidae	Bavia aericeps	Jumping spider	1
		Cosmophasis sp.	Jumping spider	2
		Euryattus sp.	Jumping spider	2
		Helpis minitabunda	Jumping spider	2
		Jacksonoides queenslandicus	Jumping spider	29
		Plotius sp.	Jumping spider	1
		Simaetha sp.	Jumping spider	1
		Tauala lepidus	Jumping spider	1
		Zenodorus orbiculatus	Jumping spider	3
	Clubionidae	Clubiona sp.	Cursorial and web-invading araneophagic spider	1
	Lamponidae	Lampona sp.	Cursorial and web-invading araneophagic spider	1

	Mimetidae	Mimetus maculosa	Web-invading araneophagous spider	1
	Araneidae	Nephilengys malabarensis	Orb-web building spider	1
	Pholcidae	Psilochorus sphaeroides	Dome-web building spider	4
		Smeringopsus sp.	Dome-web building spider	1
	Pisauridae	Inola subtilis	Sheet-web building spider	5
	Uloboridae	Philoponella sp.	Communal orb-web building spider	1
Diptera	Tipulidae	Unknown	Crane fly	1
Lepidoptera	Noctuidae	Unknown	Moth	3

and rearing from eggs. No prey spiders had prior experience with P. fimbriata and no test spiders had prior experience with either of the prey-spider species. Hunger state was standardised before testing by keeping each spider without prey for 3-5 days

Test chambers (see Fig. 1; Clark & Jackson, 1994a) were cubicle wood frames with four transparent sliding glass sides (internal dimensions of chamber: 95 mm on each side). There were four holes (diameter 15 mm) in the wooden top, kept stoppered except when introducing prey during normal feeding. There was another hole (the introduction site) centred on the wooden bottom of the cage, through which a prey spider was introduced to start a test. The test chamber set on a 95-mm cubicle base with space free for reaching the introduction site.

In nature, P. fimbriata females normally select a dead leaf (typically 20-30 mm long & 15-20 mm wide), suspend it by silk lines in the web and use it as a resting site. In the laboratory, each P. fimbriata used as a test spider was put into a clean test chamber with a dead leaf from its maintenance cage and maintained on house flies for 3-4 weeks before testing. During this time, a web was built with the leaf suspended near the top. Each female had previously oviposited, but no eggs or juveniles were on the leaf during testing.

Tests always started at 1000 hrs and ended when the prey spider was captured or at 0800 hrs the next day, whichever came first. If a test spider was not resting on its leaf at 1000 hrs when testing was scheduled, testing was postponed until the following day. Before starting a test, a prey spider (either J. queenslandicus or Helpis minitabunda) was taken into a 30-mm long (diameter, ca. 15 mm) plastic tube (one end stoppered; other open). The stopper was removed from the introduction site and the open end of the tube was positioned so that it fit flush with the inside edge of the hole in the test chamber. Next the stopper was removed from the other end of the tube and, with a small brush, the prey spider was prodded gently until it entered the chamber. Once

testing had started, introduction sites were kept plugged. During daylight hours, spiders were checked at hourly intervals, as it had been established in preliminary trials that P. fimbriata requires more than 60 min to complete feeding on these prey spiders. There were other intermittent periods of observation in addition to hourly checks.

Between tests, each glass side was removed and all parts of the chamber, including the glass sides, were washed with water and 80% ethanol, then allowed to dry before subsequent testing. This eliminated potentially confounding influences of chemical traces left by previous spiders (see Willey & Jackson, 1993).

RESULTS

Testing in the laboratory

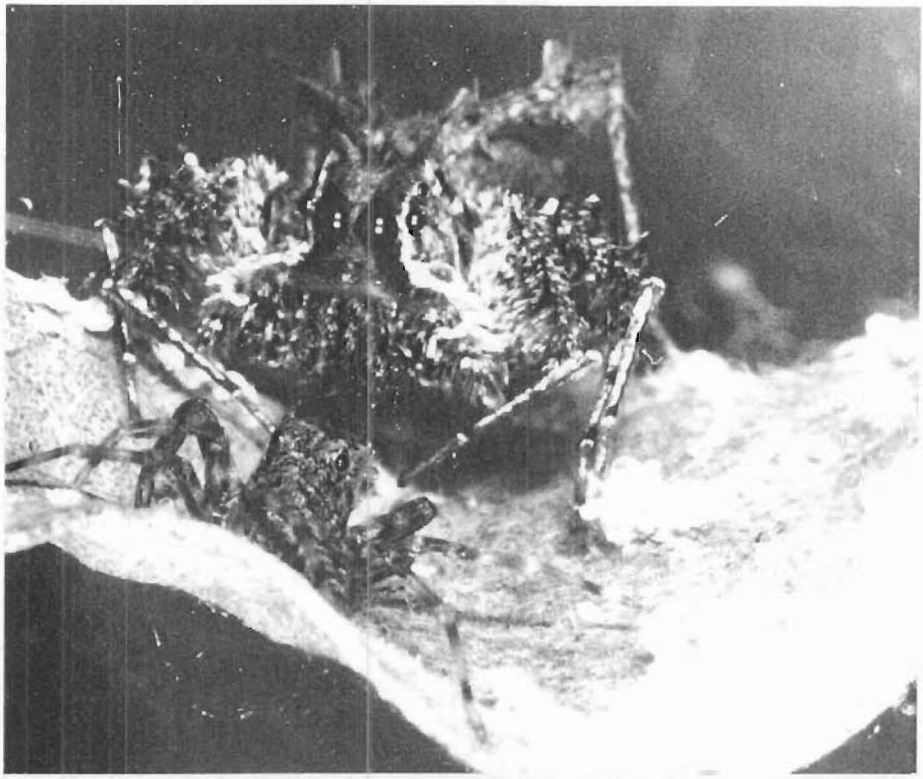
There were 79 tests (53 with J. queenslandicus; 26 with H. minitabunda), but there were no evidence that data for the two prey species differed significantly. Accordingly, data from testing with J. queenslandicus and H. minitabunda were pooled. All records of predation and interactions between spiders were from during the daylight period in the laboratory.

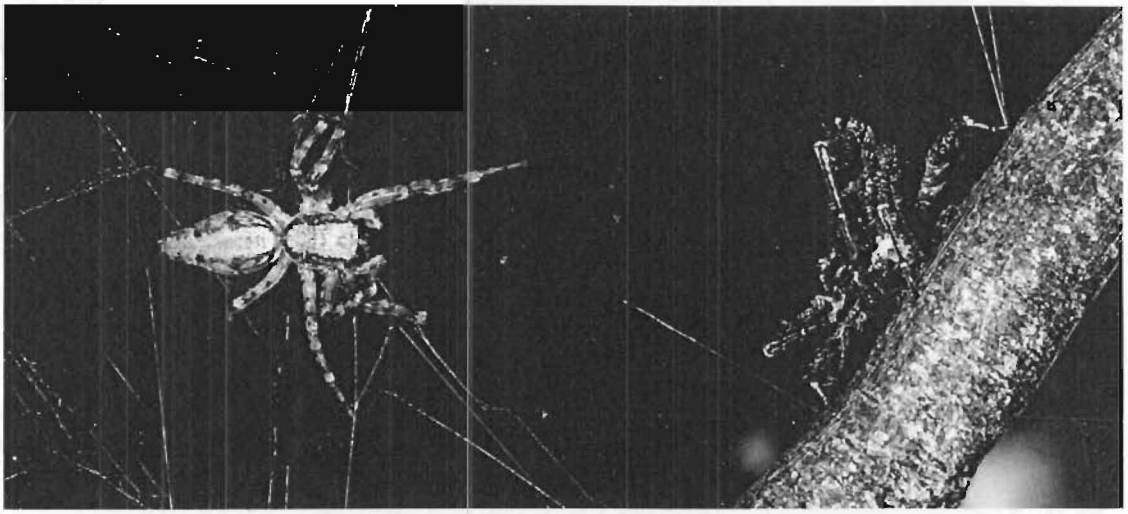
On three occasions, a H. minitabunda appeared to trip over a silk line (Fig. 1) while walking under the web. In two of these incidences, P. fimbriata was already pursing the salticid. In the other instance, P. fimbriata was initially oriented away; when the salticid contacted the silk, P. fimbriata oriented and began stalking. On three occasions (J. queenslandicus, 2; H. minitabunda, 1) a salticid leapt from outside toward a leaf but landed on the web short of the leaf. In two instances, P. fimbriata was outside the web pursing the salticid when a leap was made (Fig. 2); the

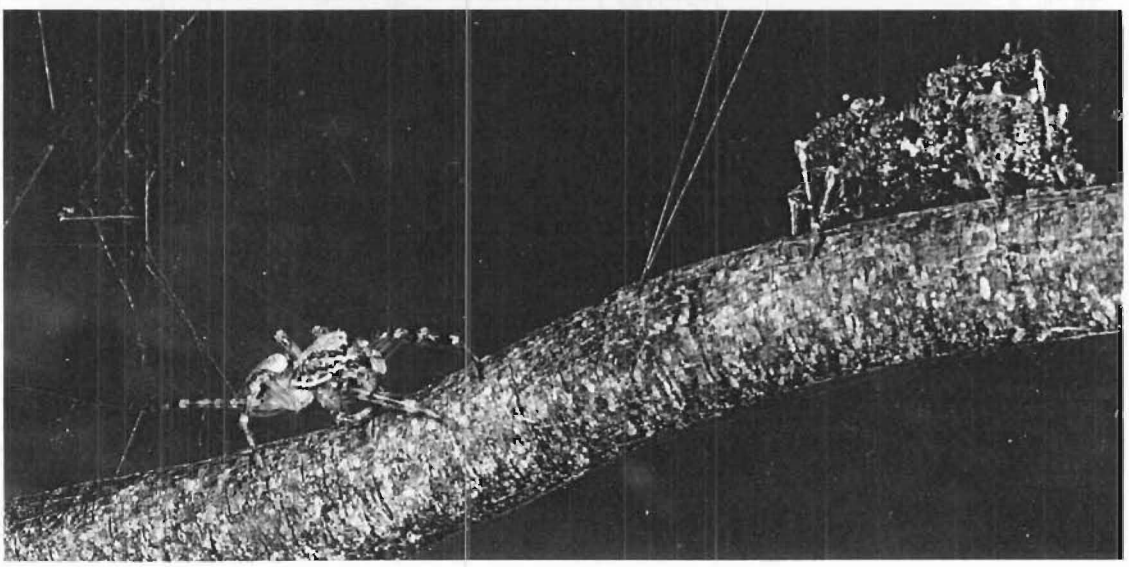
Fig. 3. Helpis minitabunda (on left in photograph) gets rear leg snagged on line in web of Portia fimbriata. Portia (right in photograph) facing and stalking Helpis. Portia on stick to which web is attached.

Fig. 2. Helpis minitabunda attempting, with difficulty, to walk across web of Portia fimbriata. Portia on stick beside web facing Helpis. Helpis on left and Portia on right in photograph. Helpis landed in the web after leaping between two sticks, and landing short.

Fig. 1. Portia fimbriata (frontal view) faces Jacksonoides queenslandicus (rear view) that had leapt from outside, onto leaf with Portia. Both spiders on leaf in Portia's web. Old silk from eggsac on leaf (visible in photograph).







salticid subsequently left the web and the sequence continued outside. In the other instance, P. fimbriata was on the leaf and not oriented toward the salticid before the leap; after the leap, the salticid left the web, P. fimbriata oriented and pursuit began.

P. fimbriata preyed on the other salticid in 35 (44%) of the tests, and prey capture was seen in 20. When first seen feeding, P. fimbriata was in its web in 18 (51%) of the 35 tests. Six categories of prey capture were discerned (Table 2).

(1) Dropped and attacked from a dragline

A prey salticid was either quiescent, standing under the web, or walking about slowly and intermittently under the web. P. fimbriata oriented toward the salticid and often there was a preliminary period during which P. fimbriata positioned itself over the salticid by moving slowly and intermittently about in the web. Eventually P. fimbriata dropped on a dragline from directly above, usually by lowering itself slowly (only 10-50 mm at a time), pausing for between several seconds and 10 min while hanging on the line, then slowly dropping again. If the salticid moved away, P. fimbriata stopped dropping, slowly turned, climbed up the line, then moved through the web until over the salticid and dropped again.

As the dropping P. fimbriata got closer and closer to the salticid, pauses became longer and more frequent. Once within 50 mm of the salticid, P. fimbriata's palps were usually retracted. Eventually, from 10-30 mm above the salticid, P. fimbriata suddenly let itself fall rapidly and inserted its fangs into the prey's dorsal body. Although P. fimbriata occasionally held on after contact, usually it stabbed (penetrated prey with fangs, but did not hold on), then moved back up the line. Whether held onto or only stabbed, the salticid went into convulsions and became immobile after 10-30 sec. After stabbing, P. fimbriata watched, then moved toward and picked up

Table 2. P. fimbriata's method of prey-capture during laboratory testing

Prey-capture Method	Tests during which prey capture was seen	Tests in which there was predation, but prey capture was not seen	Tests in which there was no predation
N	20	15	44
1. Dropped on a dragline (not seen stalking while outside web)	6 (30%)[1]	2 (13%)[2]	5 (11%)
2. Dropped on dragline, then later stalked while outside web	4 (20%)[3]	None	3 (7%)
3. Began by stalking from within web, but later stalked from outside	6 (30%)[4]	1 (7%)[5]	6 (14%)
4. Stalked outside web (stalking or dropping from in web not seen)	2 (10%)	3 (20%)[6]	9 (20%)
5. Stalked salticid while on leaf	2 (10%)[7]	2 (13%)[8]	none

[1] Attack made from dragline
[2] In web when first seen feeding
[3] Capture made outside web; 3 returned with prey to web to feed
[4] Capture made outside web; 2 returned with prey to web to feed
[5] Outside web until completed feeding
[6] Outside web when first seen with prey; 2 returned to web to feed
[7] Capture from on leaf; stayed on leaf while fed

(stalking while not on leaf, or dropping in web from a dragline, not seen)			
6. Pursuit not seen	not applicable	7 (47%)	21 (48%)

[a] On leaf when first seen with prey and until completed feeding

the immobilized prey. When picked up, the salticid was still under the web and P. fimbriata retrieved it by dropping from a dragline rather than leaving the web.

(2) Dropped on dragline, then later stalked while outside web

In these tests, P. fimbriata in a web initially dropped on a dragline, but failed to attack before the salticid moved away. After the salticid moved away, P. fimbriata left the web, stalked and eventually captured the prey.

(3) Began by stalking salticid from within web, but later stalked and captured salticid from outside

While in a web, P. fimbriata oriented toward a salticid that was outside and began stalking slowly, eventually leaving the web. The prey was eventually stalked and captured from outside the web.

(4) Stalked while outside web (stalking or dropping from in web not seen)

(5) Stalked and captured salticid while on leaf in web

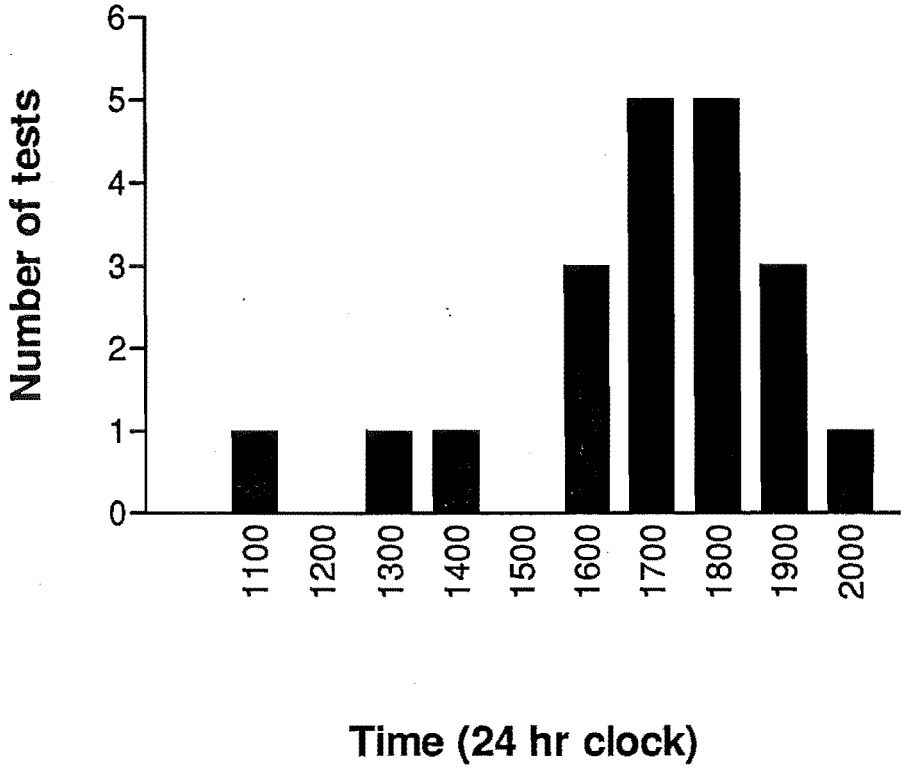
A salticid leapt from outside onto a leaf, with a P. fimbriata present but apparently not seen by the salticid. P. fimbriata slowly oriented and stalked (Fig. 3), eventually capturing the salticid on the leaf.

Comparable categories were recognised for tests during which there was no predation and during tests in which, although there was predation, the attack was not seen.

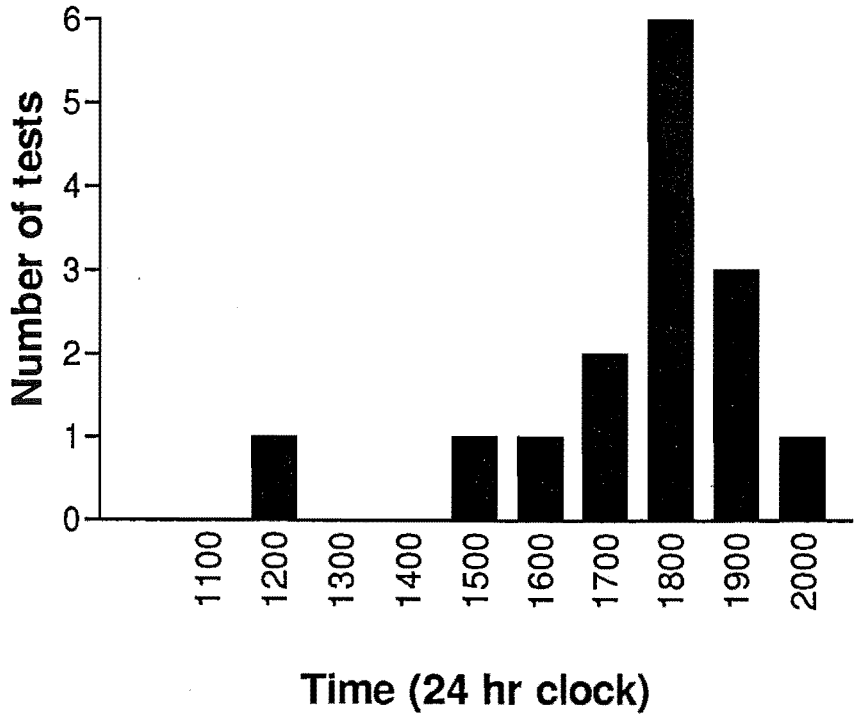
In all instances, typical cryptic stalking was adopted whenever the predator came within 50-100 mm of the prey (Fig. 3). Test spiders tended to capture prey (Fig. 4A) or were first

Fig. 4. Time when Portia fimbriata was first observed feeding on prey (A, prey capture observed; B, prey capture not observed).

A. Capture seen



B. Capture not seen



observed feeding on prey (Fig. 4B) late in the day, normally after 1600 hrs. Instances of P. fimbriata stalking and capturing salticids on leaves were always within 2 h of when lights went out in the laboratory (4 observations; 2 each at 1900 and 2000 hrs). However, there did not appear to be any particular time at which spiders were first seen pursuing prey (Fig. 5).

DISCUSSION

P. fimbriata has acute vision and complex vision-mediated predatory behaviour (Jackson & Wilcox, 1998). Typical web building spiders from other families, having simple eyes and only rudimentary eyesight, rely primarily on web signals (tension and vibration patterns of web-silk lines) for locating and identifying prey. Besides serving as a critical component of the typical web builder's sensory system (Witt, 1973, Witt & Rovner, 1982), webs may also attract and ensnare, or at least temporarily detain, prey (Craig & Bernard, 1990; Craig et al., 1994, 1996; Shear, 1994; Tso, 1998).

P. fimbriata's web may also attract prey, but P. fimbriata's prey is unusual. Unlike other web-building spiders, which tend to be primarily insectivorous, P. fimbriata is araneophagic. The predominance of spiders in P. fimbriata's diet suggests that the insects trapped in P. fimbriata's web might serve, not so much as food, but rather as lures to attract other spiders. By using trapped insects this way, P. fimbriata does not have to leave its web to catch prey, as neighbouring web-building spiders will come into P. fimbriata's web (Jackson & Blest, 1982a).

P. fimbriata takes salticids in preference to non-salticid spiders when outside webs (Li & Jackson, 1996a), and our field data for P. fimbriata in their own webs are consistent. Feeding on salticids was recorded almost three times more often than feeding on non-salticid spiders.

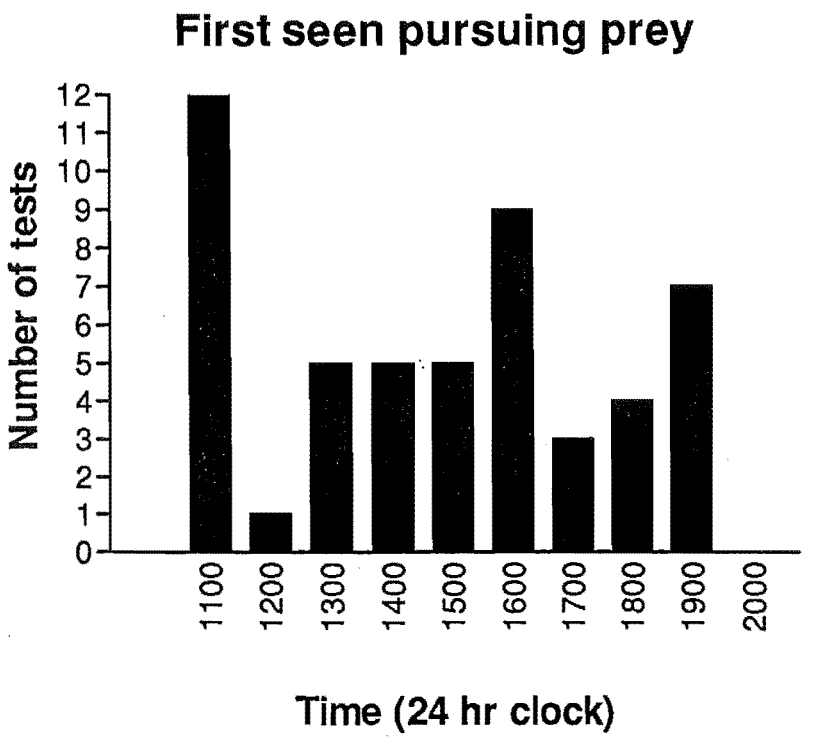


Fig. 5. Time when Portia fimbriata was first observed pursuing prey.

Jacksonoides queenslandicus was by far the most frequently recorded prey species accounting for 69% of the records of feedings on salticids and for 47.5% of records for all species. Part of the explanation must be J. queenslandicus's exceptionally high abundance in the Queensland habitat of P. fimbriata, but another factor may also be important: J. queenslandicus's propensity to frequent the vicinity of webs, sometimes entering them to capture prey or to take up residence on detritus (Jackson, 1988). The web serves as a platform from which P. fimbriata can detect and drop onto J. queenslandicus, and other salticids, but the web may also function as something like a trap because J. queenslandicus tends to enter the web where it becomes P. fimbriata's prey.

CHAPTER 5:

SPECULATIVE HUNTING BY AN ARANEOPHAGIC SALTICID SPIDER

ABSTRACT

Portia fimbriata, an araneophagic jumping spider (Salticidae), makes undirected leaps (erratic leaping with no particular target being evident) in the presence of chemical cues from Jacksonoides queenslandicus, another salticid and a common prey of P. fimbriata. Whether undirected leaping by P. fimbriata functions as hunting by speculation is investigated experimentally. Our first hypothesis, that undirected leaps provoke movement by J. queenslandicus, was investigated using living P. fimbriata and three types of lures made from dead, dry arthropods (P. fimbriata, J. queenslandicus and Musca domestica). When a living P. fimbriata made undirected leaps or a spring- driven device made the lures suddenly move up and down, simulating undirected leaping, J. queenslandicus responded by waving its palps and starting to walk. There was no statistical evidence that the species from which the lure was made influenced J. queenslandicus' response in these tests. Our second hypothesis, that J. queenslandicus reveals its location to P. fimbriata by moving, was investigated by recording P. fimbriata's reaction to J. queenslandicus when J. queenslandicus reacted to lures simulating undirected leaping. In these tests, P. fimbriata responded by turning toward J. queenslandicus and waving its palps.

INTRODUCTION

A general problem facing predators is how to locate prey (Curio, 1976). When vision is

relied on, being out of the predator's line of sight or being camouflaged will interfere with detection (Edmunds, 1974). "Hunting by speculation" (directing attacks at refuges where prey tend to be found or probing areas in which prey normally hide) is a potential solution (Curio, 1976). Envisaged not as prey-capture behaviour, but instead as a tactic for locating prey, hunting by speculation might function for a predator by provoking a response that reveals the prey's location. Woodstorks, for example, may probe submerged vegetation even when no prey is visible (Kahl & Peacock,1963), Octopus cyanea Gray attacks holes in coral even in the absence of prey (Yarnell, 1969) and lions may run to the top of hills, apparently in anticipation of startling unwary prey on the other side (Schaller, 1972). However, examples from arthropods, and experimental studies on any predator, have been scarce.

In the present paper, we investigate hunting by speculation in Portia fimbriata (Doleschall) from Queensland, Australia (Jackson & Wilcox, 1998), an araneophagic jumping spider (Salticidae) that preys especially often on other salticids (Jackson & Blest, 1982a). Jacksonoides queenslandicus Wanless (Salticidae) is especially abundant in the same habitat as P. fimbriata (Jackson, 1988) and is probably the salticid species on which P. fimbriata most often preys. Chemical cues from J. queenslandicus, even in the absence of J. queenslandicus, prepare P. fimbriata for predation by stimulating the adoption of a special palp posture (retracted palps) characteristic of stalking sequences against salticids as prey and by heightening P. fimbriata's attention to optical cues from J. queenslandicus. Chemical cues from J. queenslandicus also elicit intermittent undirected leaps by P. fimbriata (Clark & Jackson, unpubl. data). The absence of an apparent target suggests that this behaviour functions as speculative hunting. Two hypotheses are considered here: (1) undirected leaps by P. fimbriata stimulate J. queenslandicus to move; (2) by moving, J. queenslandicus gives away its location

to P. fimbriata.

METHODS

General

Standard maintenance procedures in a controlled-environment laboratory (light-dark cycle, 12L:12D; lights on at 0800 h) were adopted, as detailed elsewhere (Jackson & Hallas, 1986b). Adult females of P. fimbriata and J. queenslandicus (body length: P. fimbriata 10-11 mm; J. queenslandicus 5-6 mm), from laboratory cultures, were used.

Experiment 1. J. queenslandicus viewing P. fimbriata

These tests were used to get baseline information on how J. queenslandicus reacted when P. fimbriata made undirected leaps. For a test chamber, we used a transparent perspex box (length X width X height: 211 mm X 144 mm X 44 mm). Three regions of the box were defined: region 1 extended 50 mm out from one end of the box; region 2 extended 50 mm out from the opposite end; region 3 was the space between the other two regions. There was a 5-mm wide hole (kept plugged with a cork) in the bottom of the box in the centre of region 1 and another in the centre of region 2. Before testing began, two opaque plastic partitions were in place: partition 1 between region 1 and 3; partition 2 between region 2 and 3. Test spider No. 1 (J. queenslandicus) was in region 1 and test spider No. 2 (P. fimbriata) was in region 2.

Test spider 1 was put in the box 24-28 h before testing started and had free access to the three regions. Testing began between 0800 h and 1000 h. When test spider 1 was within 50

mm of one end of the box, partition 1 was put into place, thereby closing region 1 off from the rest of the box. Partition 2 was also put into place, closing off region 2. Test spider 2 was introduced 10 min later into region 2 through the hole in the bottom of the cage. For transfer, first test spider 2 was enticed into a plastic tube (diameter 5 mm), then the tube was positioned with one end against the hole in the test chamber. When gently prodded by inserting a soft brush through the other end of the tube, test spider 2 walked slowly out into the test chamber.

Testing began only if J. queenslandicus had remained quiescent for the previous 5 sec facing region 2. With J. queenslandicus quiescent, partition 2 followed by partition 1 was removed. The behaviour of the two spiders was observed for the next 10 min. Control tests were the same as experimental tests except that partition 2 remained in place (i.e., J. queenslandicus could not see P. fimbriata during these tests).

Being interested specifically in how J. queenslandicus reacted to undirected leaping by P. fimbriata, we consider only those experimental and control tests in which: 1) P. fimbriata made a single undirected leap during the 10-min test interval and 2) J. queenslandicus remained quiescent for the entire period prior to P. fimbriata making its undirected leap. The test was aborted if: 1) P. fimbriata moved during an experimental test into region 3 before making an undirected leap or 2) P. fimbriata made a second undirected leap before the 10-min test interval elapsed. No individual J. queenslandicus or P. fimbriata was used in more than one successful test. Different individuals were used in experimental and control tests.

Experiment 2. J. queenslandicus viewing a lure

Our objective was to test simultaneously how J. queenslandicus reacted to a moving lure (a simulation of undirected leaps by P. fimbriata) and how P. fimbriata reacted to J. queenslandicus' reaction to the lure. The test chamber (Fig. 1) was a rectangular perspex box (length X width X height: 147 X 51 X 51 mm) with two tubes. Its design permitted viewing of a lure by J. queenslandicus and viewing of J. queenslandicus by P. fimbriata.

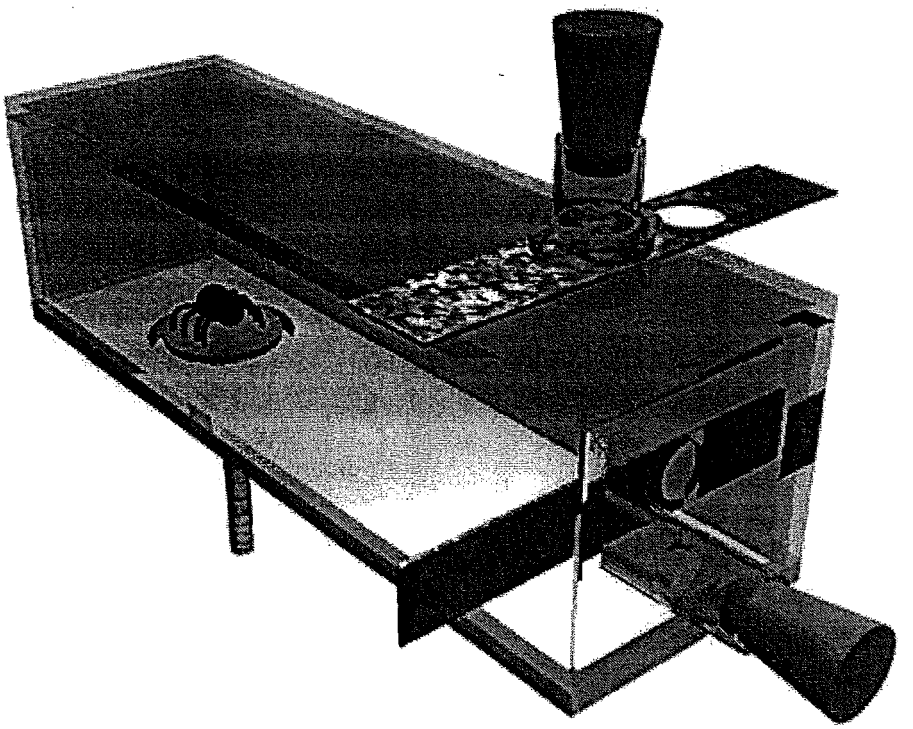
Tube 1 (internal diameter 13 mm), made of transparent glass, fit inside the box at one end (Fig. 1). Except when introducing J. queenslandicus the hole opening to the outside was kept stoppered. Initially, a hole at the opposite end of the tube was blocked by an opaque metal screen (partition 1). This screen, which fit into a slit in the box, could be moved from side to side. On the side of the box opposite tube 1, tube 2 (internal diameter 13 mm) housed P. fimbriata. The distal opening of tube 2 was kept stoppered except when introducing test spider 2. The proximal opening of tube 2 opened into a wider tube (internal diameter 20 mm) which in turn opened into the box. An opaque metal screen (partition 2) covered the opening between the narrow and wide tube. This screen fit into a slit in the wider tube, and it could be moved from side to side. The wide tube was positioned so that its centre was directly across from where tube 1 opened into the interior of the box.

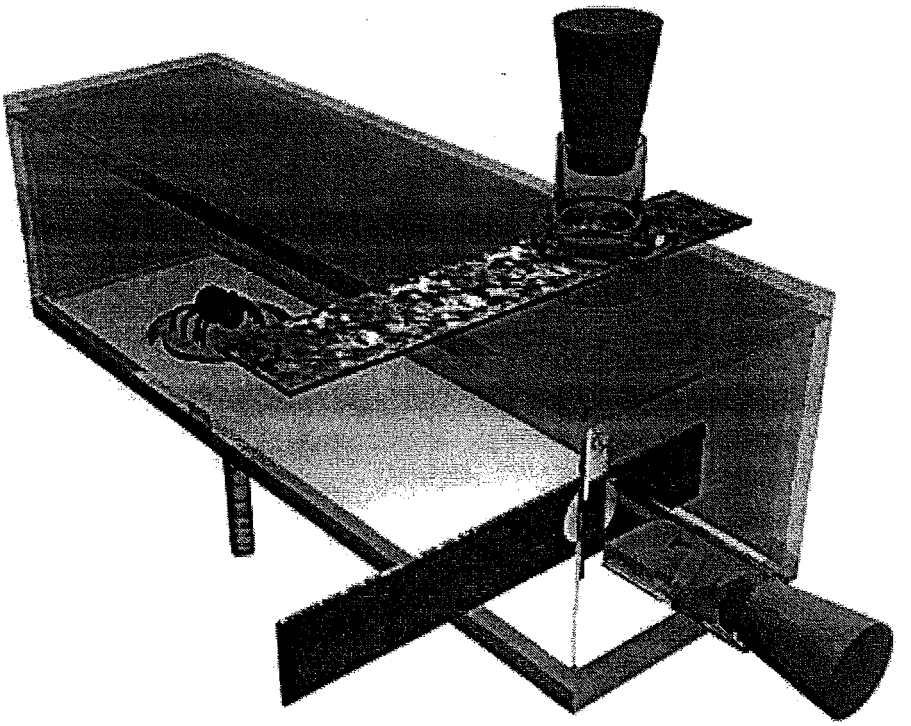
In front of tube 1, there was a hole through which a lure could move (Fig. 1). Each lure was made by positioning a dead J. queenslandicus, P. fimbriata or house fly (Musca domestica Linnaeus) in a lifelike posture on a cork disk (diameter 17 mm; height 22 mm). The dead arthropod was then sprayed with an aerosol plastic adhesive (Crystal Clear Lacquer, Atsco Australia Pty.) for preservation and to mask any chemical traces that might have remained on the dead arthropod.

Undirected leaps were simulated using a 'leap generator' (a metal stylus moved by an

Fig. 1.Apparatus allowing test spider to view leaping lure: (A) 'Exploded' diagram of apparatus. (B) Assembled cage, with tubes blocked as during introduction of test spider. (C) Assembled cage, with tubes unblocked as during test. Lure on top of wooden rod, connected to an electric motor ('leap generator', not shown). Abbreviations used in Fig. 1A: external opening of tube 1 (EO1); external opening of tube 2 (EO2); hole in partition 1 (HP1); internal opening of tube 1 (IO1);internal opening of tube 2 (IO2); internal opening of wide tube (IOW); hole in end piece of box (HB); slit 1 (SL1); slit 2 (SL2); stopper 1 (ST1); stopper 2 (ST2); wide tube (WT)). See text for details.

ST2
EO2
Tube 2
HP2
IOW
IO2
Lure
Partition 2
WT
Cork Disc
SL2
Rod in Elevated Position
End Piece of Box
HB
HP1
EO1
ST1
SL1
IO1
Partition 1
Tube 1





electric motor and a spring). When activated, the motor pulled the stylus (stretching the spring) down 10-mm against an electromagnet. When a switch was pushed, the electromagnet was temporarily disabled, letting the spring suddenly move the stylus 10 mm back up to its original position, after which the electric motor immediately moved the stylus back against the reactivated electromagnet.

A wooden rod connected the lure to the leap generator. One end of the rod (80 mm long and 1 mm thick) was glued to the centre of the bottom of the cork disk holding the lure. The other end of the rod was glued at right angles to the distal end of the stylus. Before testing began, the stylus was held in place by the magnet and the lure was positioned just below the hole in the cage, facing tube 1. The quiescent lure remained out of the test spiders' view even after tube 1 was uncovered because the bottom of the cage was opaque.

In each partition there was a hole equal in size to the opening of the tube it blocked. Tubes were unblocked (Fig. 1C) by first moving partition 1 slowly to where its hole was aligned with the opening of tube 1, providing access to the interior of the box. Next, partition 2 was moved slowly so that its hole was aligned with the opening of tube 2, providing access to the wider tube that opened into the box. Partitions were moved only when the following criteria were met: 1) both spiders were quiescent; 2) both were facing the proximal opening of the tube (i.e., both were facing into the interior of the box); 3) both had been quiescent for the previous 5 sec. If, after partition 2 was removed, both test spiders remained quiescent for the next 5 sec, testing began by pushing the switch to make the lure spring upward 10 mm into the box. The behaviour of the two test spiders was recorded for the following 30 sec.

Testing was aborted if (1) either spider failed to become quiescent while facing the specified direction within 2 h of being placed into its tube or (2) either spider moved during the

interval between moving the partitions (unblocking tubes) and making the lure leap. When tests were aborted, the same two spiders were tested on subsequent days until a successful test was achieved or four successive days of unsuccessful testing elapsed.

Control tests were identical to tests during which lures were made to leap except that the lure (P. fimbriata) was positioned 10 mm further below the hole in the box so that it remained below the opaque surface of the box when the switch was pushed. This meant that, in control tests, potential cues that might have come from sound or substrate vibration were still present, but optical cues from the lure were absent. During control tests, the behaviour of both spiders was recorded for 30 sec starting 5 sec after partition 2 was removed.

No individual J. queenslandicus or P. fimbriata was used in more than one successful test, and different individuals were used in tests with each of the three types of lures and in controls.

RESULTS

Experiment 1. J. queenslandicus viewing P. fimbriata

There were 14 experimental tests in which P fimbriata made one undirected leap. In five of these tests, J. queenslandicus remained quiescent for the remainder of the test ('no reaction'). P. fimbriata showed no recognisable reaction to these five J. queenslandicus. In the other nine tests, J. queenslandicus oriented toward P. fimbriata and began to wave its palps up and down within 2 sec after P. fimbriata leapt. Subsequently, eight of these J. queenslandicus began to walk about, but the other J. queenslandicus remained in place for 145 sec, with palps

waving intermittently, then became quiescent (P. fimbriata oriented toward this J. queenslandicus). In one test, J. queenslandicus waved its palps, then walked about after the undirected leap, but there was no evidence that P. fimbriata reacted to J. queenslandicus' movement. In the other seven tests, P. fimbriata oriented when J. queenslandicus became active. In three instances, this was after J. queenslandicus began to walk. In the other four instances, it was while J. queenslandicus was waving its palps but before beginning to walk.

There were nine control tests in which P. fimbriata (not visible to J. queenslandicus) made one undirected leap. Jacksonoides queenslandicus remained quiescent in each. Compared to when in control cages, J. queenslandicus was significantly more likely to begin walking about and waving palps if a leaping P fimbriata was visible (X^2 test of independence, $P<0.01$).

Experiment 2. J. queenslandicus viewing a lure

Jacksonoides queenslandicus became active (walked and waved its palps) in tests where a leaping lure was visible significantly more often than in control tests (Fisher's exact test, Table 1). There was no statistical evidence (tests of independence, all NS) that the type of lure used influenced whether J. queenslandicus or P. fimbriata became active during tests, nor was there statistical evidence that the presence or type of lure influenced whether J. queenslandicus or P. fimbriata left their respective tubes during tests. However, the behaviour of both J. queenslandicus and P. fimbriata differed depending on whether or not lures were visible to J. queenslandicus.

There were 15 successful control tests. Jacksonoides queenslandicus and P. fimbriata

Table 1. Number of tests in which Jacksonoides queenslandicus and Portia fimbriata became active (walked and waved palps), and left tubes, when lure moved in experiment 2 (Jacksonoides queenslandicus viewing a lure and Portia fimbriata viewing J. queenslandicus). Compared with control (no lure visible), both Jacksonoides queenslandicus and Portia fimbriata more often became active when moving lure was visible to J. queenslandicus.

Type of testing	N	Jacksonoides queenslandicus becomes active	Portia fimbriata becomes active	Jacksonoides queenslandicus left tube 1	Portia fimbriata left tube 2
Control	15	3	3	3	1
Portia fimbriata lure	18	14***	15***	4	1
Jacksonoides queenslandicus lure	14	9*	9*	3	3
House fly lure	17	14***	15***	3	3[2]

[2] Results of X^2 test of independence, with Bonferroni corrections, comparing data from tests with each type of lure (Rows 2-4) to data from control tests (Row 1). All comparisons of data from testing any one type of lure with each other type of lure: NS.
* P<0.05. **P<0.01. ***P<0.005.

both remained quiescent in 12 (Table 1). In three, J. queenslandicus walked out of tube 1. When this happened, P. fimbriata waved its palps, then stayed in tube 2 in two instances and left tube 2 and entered the wide tube in one instance. No Portia entered the box.

There were 18 successful tests using lures made from P. fimbriata (Table 1). In three, both test spiders remained quiescent during the 30-sec testing interval. In one, P. fimbriata left tube 2 and entered the wide tube 145 sec after the lure was made to leap, but J. queenslandicus remained quiescent. There were 11 tests in which J. queenslandicus waved its palps about 5 sec after the lure was made to leap. In eight of these, J. queenslandicus stayed in the tube, intermittently waving its palps. The other three J. queenslandicus walked slowly out of the tube and into the box, intermittently waving their palps. Another three J. queenslandicus remained quiescent for 15-60 sec after the lure was made to leap, then began waving their palps. One of these subsequently walked out of the tube. In every test in which J. queenslandicus waved its palps, P. fimbriata reciprocated by waving its palps. In one of these tests, P. fimbriata subsequently left tube 2 and went into the wide tube.

There were 14 successful tests using lures made from J. queenslandicus (Table 1). In five, both test spiders remained quiescent during the 30-sec testing interval. There were nine tests in which J. queenslandicus waved its palps within 5 sec after the lure was made to leap. Six of these J. queenslandicus stayed in the tube, intermittently waving their palps. The other three intermittently waved their palps while walking slowly out of the tube and into the box. In all of the tests in which J. queenslandicus waved its palps, P. fimbriata afterwards began waving its palps. In three of these tests, P. fimbriata subsequently left tube 2 and went into the wide tube.

There were 17 successful tests using lures made from a house fly (Table 1). In two,

both test spiders remained quiescent during the 30-sec testing interval. In one, J. queenslandicus remained quiescent, but P. fimbriata left tube 2 and entered the wide tube. There were 13 in which J. queenslandicus waved its palps within 5 sec after the lure was made to leap. Ten of these 13 J. queenslandicus stayed in the tube, intermittently waving their palps. The other three intermittently waved their palps while walking slowly out of the tube and into the box. One J. queenslandicus remained quiescent for 15 sec after the lure was made to leap, then began waving its palps. In all of the tests in which J. queenslandicus began waving palps, P. fimbriata afterwards began waving its palps. In two of these tests, P. fimbriata subsequently left tube 2 and went into the wide tube.

DISCUSSION

Salticids can detect motionless prey (Jackson & Tarsitano, 1993), but movement facilitates prey detection and stimulates the salticid to begin predatory sequences earlier (Heil, 1936; Crane, 1949; Drees, 1952; Jackson & Tarsitano, 1993). Our hypothesis is that undirected leaps function to enhance P. fimbriata's ability to locate J. queenslandicus: leaps, by attracting attention, elicit palp waving and walking by J. queenslandicus, which in turn provides movement cues P. fimbriata can use to locate J. queenslandicus. Our findings support this hypothesis.

In experiment 1, J. queenslandicus more often waved its palps and walked when undirected leaps by P. fimbriata could be seen. In control tests, when P. fimbriata's undirected leaps could not be seen, J. queenslandicus tended to remain quiescent. Experiment 2 also demonstrated that J. queenslandicus' reaction to undirected lures tends to attract P. fimbriata's

attention.

Seeing lures make simulations of undirected leaps in experiment 2 elicited comparable reactions from J. queenslandicus, regardless of whether the lures were made from P. fimbriata, J. queenslandicus or house flies. These findings suggest that J. queenslandicus' response is a generalised investigatory behaviour provoked by an unidentified object moving in the neighbourhood and not a reaction specifically to P. fimbriata.

P. fimbriata appears to test the environment for the presence of J. queenslandicus by attempting to provoke, with undirected leaps, a response from its not-yet-seen prey. Undirected leaps differ from how octopuses and wood-storks flush out prey by attacking the prey's microhabitat (Yarnell, 1969; Kahl & Peacock, 1973) because P. fimbriata appears not to focus on a target when it leaps. P. fimbriata's undirected leaps appear to be more comparable to a lion running up a hill in anticipation of startling unwary but not-yet-seen prey (Schaller, 1972).

Curio (1976) with the term 'speculative hunting' outlined a general mechanism for how prey might be located. Details about the role of any particular behaviour in a predator's repertoire, or precisely how speculative hunting worked, were not considered. For P. fimbriata, we have details concerning the cues that provoke speculative hunting and the manner in which undirected leaping is used by P. fimbriata to find its prey.

The stimuli governing speculative hunting by other predators are not well understood, but P. fimbriata's undirected leaping is stimulated by chemical cues from a specific prey. The leap itself is not prey-capture behaviour, because undirected leaps are not seen after P. fimbriata has located its prey. Instead, this tactic can be envisaged as something more akin to setting a trap. Triggered by chemical cues, undirected leaping is still speculative because

chemical cues do not guarantee the presence of J. queenslandicus in the immediate vicinity. Undirected leaps provide the prey with optical cues and prey in turn provide the predator with optical cues. By soliciting optical cues in response to chemical cues, P. fimbriata appears to co-ordinate sensory modalities.

Still other facets of P. fimbriata's predatory strategy may qualify as speculative hunting. Females of Euryattus sp., another salticid on which P. fimbriata preys, nest in a rolled-up dead leaf suspended by silk guylines from tree trunks, boulders or the vegetation (Jackson, 1985). To catch Euryattus females, P. fimbriata simulates the courtship signals used by Euryattus males (Wilcox & Jackson, 1998). Upon finding a conspecific female's nest, a Euryattus male goes down the guylines and signals by suddenly and forcefully flexing his legs, thereby making the leaf rock back and forth. Euryattus females react to the male's signal by coming out of the nest and either mating with the male or driving him away. When P. fimbriata locates a nest, a similar sequence is seen. Portia fimbriata moves to a position above the suspended leaf, then either lowers itself on its own dragline or walks down one of Euryattus' guylines. Once on the leaf, P. fimbriata uses a special behaviour, 'shuddering', which mimics the courtship of Euryattus males and induces the resident to come out (Jackson & Wilcox, 1990). Interestingly, P. fimbriata will shudder even when no Euryattus is present, suggesting that this behaviour has an investigatory function. When shudders provoke a response from a resident inside a rolled up leaf, P. fimbriata continues the predatory sequence. When no reply is forthcoming, P. fimbriata desists from signalling (Jackson et al., 1997).

Besides preying on salticids, P. fimbriata also preys on web-building spiders from other families. Portia fimbriata enters the other spider's web and, instead of simply stalking or chasing down the resident, makes aggressive mimicry signals (Jackson & Wilcox, 1998). For

example, by manipulating the web silk with its legs and palps, P. fimbriata may lure the resident spider to within striking distance by imitating the struggles of an insect on the web (Jackson & Blest, 1982a). However, P. fimbriata will initiate signalling even when a resident is not visible (Jackson, 1995), suggesting that aggressive-mimicry signals may sometimes function as hunting by speculation.

Like undirected leaping, initiating aggressive mimicry signals in another spider's web, or on a suspended leaf of Euryattus with no resident visible, may attract the attention of a prey that P. fimbriata has not yet seen. By responding with investigatory behaviour to P. fimbriata's aggressive-mimicry signals, the prey may be induced to give away its location. Undirected leaping sends optical cues to potential prey, whereas web signals and shuddering on a leaf send vibratory cues to potential prey, and this may be the primary difference.

Not only might aggressive-mimicry signals sometimes be envisaged as speculative hunting, but undirected leaping might be envisaged as aggressive mimicry because undirected leaping may simulate the kinds of optical cues that normally elicit investigation by J. queenslandicus. For example, the initial cues J. queenslandicus might normally get from an insect (potential prey) or a conspecific individual (potential mate or rival) may not be so different from the cues provided by P. fimbriata's undirected leaping. In P. fimbriata's predatory strategy, speculative hunting and aggressive mimicry appear to be broadly overlapping topics.

CHAPTER 6:

CHEMICAL CUES FROM ANTS INFLUENCE PREDATORY BEHAVIOUR IN HABROCESTUM PULEX (HENTZ), AN ANT EATING JUMPING SPIDER (ARANEAE, SALTICIDAE).

Abstract: The ability of Habrocestum pulex, a myrmecophagic jumping spider, to detect olfactory and contact chemical cues from ants was investigated experimentally. When given a choice between walking over clean soil or soil that had housed ants, H. pulex spent significantly more time on ant-treated soil. However, H. pulex did not appear to discriminate between clean blotting paper and blotting paper over which ants had walked. In tests using a Y-shaped olfactometer, when given a choice between an experimental arm containing air from a cage containing ants, or 6-methyl-5-hepten-2-one, and a control arm containing clean air, H. pulex moved into the experimental arm significantly more frequently than the control arm. When on soil that had previously housed ants, agitated walking, undirected leaping, posturing with body elevated, and perching on top of corks were each significantly more prevalent than when H. pulex was on clean soil. Chemical cues left by ants on soil also affected H. pulex's attention to visual cues from ants: when on treated soil, H. pulex initiated and completed stalking sequences more often, and after shorter latency, than when on control soil.

INTRODUCTION

Unique, complex eyes and acute vision in jumping spiders (Salticidae) have led to the

evolution of intricate, vision-guided courtship and predatory tactics (Crane, 1949; Drees, 1952; Land, 1969a, b; Forster, 1982; Blest et al., 1990; Jackson & Pollard, 1996, 1997). However, salticids are not restricted to reliance on optical cues, as tactile, auditory, chemical, and substrate-vibration cues also influence salticid courtship, either concurrent with or as alternatives to visual communication (Richman & Jackson, 1992; Jackson & Pollard, 1997). Pheromone-based intraspecific communication is widespread in the Salticidae (Jackson, 1987; Pollard et al., 1987; Willey & Jackson, 1993; Clark & Jackson, 1994a, b, 1995a, b), but little is known about whether salticids are influenced by kairomones (chemicals that provoke a response beneficial to the receiver but not the sender of the signal, where the sender and receiver belong to different species: Brown et al., 1971).

Ants are one of the most abundant prey-size arthropods in the habitats of most spiders (Hölldobler & Wilson, 1990), but their defences (strong mandibles, formic acid and poison-injecting stings: Wray, 1670; Edmunds, 1974; Hölldobler & Wilson, 1990; Blum 1992) appear to present spiders with formidable challenges. Yet a minority of spiders has overcome the ant's defences, thereby gaining access to this exceptionally numerous prey (MacKay, 1982; Oliviera & Sazima, 1985; Nyffeler et al., 1988; Elgar, 1993; Cushing, 1997).

Within the Salticidae, 21 ant-eating (myrmecophagic) salticids have been studied in detail: Aelurillus aeruginosus (Simon), A. cognatus (O.P.-Cambridge), A. kochi Roewer, six undescribed species of Chalcotropis Simon, Chrysilla lauta Thorell, Corythalia canosa (Walckenaer), Habrocestum pulex (Hentz), Siler semiglaucous Simon, Siler sp. Simon, Natta rufopicta Simon, three undescribed species of Natta Karsch, and two undescribed species of Xenocytaea Berry, Beatty, Prozynski(formerly called 'Euophrys'), Zenodourus orbiculatus (Keyserling) (Edwards et al., 1974; Cutler, 1980; Jackson & van Olphen, 1991, 1992; Li et al., 1996; Jackson et al., 1998). Although these species feed on a wide variety of insects, they have all been shown in standardised

tests to prefer ants over other prey and to have ant-specific prey-capture behaviour (Li & Jackson, 1996b). Except for Corythalia canosa and Zenodourus orbiculatus, each of these species has been shown to prefer ants as prey and to use ant-specific prey-capture behaviour even when tested with motionless lures (dead insects mounted in life-like posture on corks), implying that optical cues pertaining to shape and form enable them to distinguish ants from other insects (Li & Jackson, 1996b; Li et al 1996; Jackson et al. 1998). However, the ability to rely solely on vision for detecting ants does not preclude the possibility that chemical cues also influence the predatory behaviour of myrmecophagic salticids.

In the present paper, we investigate how Habrocestum pulex, a previously studied myrmecophagic salticid from North America, responds to chemical cues from ants. Habrocestum pulex lives in leaf litter, a microhabitat in which numerous visual obstructions might often hinder early visual detection of prey. Ability to detect chemical cues from ants might play an important role in preparing H. pulex to respond appropriately to its unusually dangerous prey.

In earlier studies (Cutler, 1980; Li et al., 1996), H. pulex was tested with prey in a simple laboratory environment. In the present study, we first observe H. pulex's predatory behaviour in an environment with leaf litter present, thereby simulating nature more closely than previously. We next consider three hypotheses concerning how H. pulex might react to contact chemical cues when in an environment recently occupied by ants. Habrocestum pulex might do any combination of the following: remain in that environment, adopt behaviour and posture appropriate for capturing ants, or exhibit heightened attention to optical cues from ants. We consider the role of both olfactory and contact chemical cues from ants in moderating the prey-capture behaviour of H. pulex.

METHODS

General.-- Except for minor modifications, maintenance procedures, cage design and data analysis were as in earlier studies (Jackson & Hallas, 1986a). All experiments were carried out in New Zealand using laboratory cultures of H. pulex, originally collected in Kansas, U.S.A. Each individual salticid was used in a maximum of two tests for any one experiment and there was no evidence that the identity of individual salticids influenced test outcome. Data from males and females, not being statistically different, were pooled. Body lengths of adults were 3-5 mm. Statistical methods were from Sokal & Rohlf (1995).

In observations and experiments with live ants, we used Monomorium antarcticum Smith, a myrmicine ant native to New Zealand (Ettershank, 1966, Bolton,1987). The most common prey of H. pulex in nature appear to be Lasius spp. (Formicinae) (Cutler, unpub.), which were not available in New Zealand. To test for responses which might be specific to Lasius spp., we conducted olfactometer tests using commercially available 6-methyl-5-hepten-2-one (Sigma Chemical Co.), an alarm pheromone of Lasius spp. and other ants (Cavill et al., 1956; Trave & Pavan, 1956; Bernardi et al., 1967; McGurk et al., 1968; Bergström & Löfqvist, 1968, 1970; Duffield et al., 1977; Türker, 1997a,b). Monomorium antarcticum and other myrmicine ants appear not to make this pheromone (Hölldobler & Wilson, 1990).

Predation on ants in a complex environment.-- The environment was a plastic box (length 170 mm, width 110 mm, depth 60 mm) filled to a depth of 15 mm with soil. Leaf litter was scattered about on top of the soil, covering about 30% of the box surface. Four small corks on which H. pulex could stand were spaced within the box, providing perches above the level of leaf litter. Observations were staged by putting H. pulex in this environment in the presence of 10-20 prey, where (depending on the test) prey were either ants or vestigial-winged fruit flies (Drosophila melanogaster Meigen). The goal was to get qualitative information on how H. pulex captured prey in approximately natural environments.

Choice tests using blotting paper.-- We adopted, after minor modification, procedures devised earlier for testing the ability of salticids to discriminate between the draglines of different conspecific individuals (Clark & Jackson, 1994a, 1995a, b). In each test, H. pulex was offered a choice between treated (had been in contact with ants) and untreated (clean) blotting paper. Treated blotting paper was prepared by leaving four ants in a plastic petri dish (diameter 90 mm) for 2 h, with one circular piece of blotting paper taped to the top and another to the bottom. During the 2-h period, ants actively walked about in the petri dish, repeatedly moving over both pieces of blotting paper.

Immediately afterward, each piece of blotting paper was cut in half and the test chamber was prepared. The test chamber was another petri dish (diameter 90 mm) with one half piece of treated blotting paper taped to the top of the dish and another half piece of treated blotting paper taped to the bottom of the dish directly below the top piece. The other half of the test chamber had control blotting paper taped to the top and bottom. A 15-mm triangle, cut out of the blotting paper and surrounded by a horseshoe-shaped metal divider, served as a "neutral area" into which the test spider was introduced before testing. Having the divider in place meant that the salticid could not, all at once, view the entire space within the petri dish (see Clark & Jackson 1994a). A test was defined as having started when the spider moved out of the neutral area and onto the blotting paper. This always happened within 1 min. The test ended 10 min later. For each test, a difference score was obtained (time spent on treated paper minus time spent on control paper). Maximum and minimum possible scores were + 600 sec (spent entire time on ant-treated blotting paper) and -600 sec (spent entire time on control blotting paper), respectively.

Choice tests using soil.-- Commercial potting mix was placed in a square (160 mm X 160 mm, height 80 mm) plastic storage container filled to a depth of 20 mm and microwaved (900 W) for 10 min, then held in the container (kept closed) for a waiting period of 20-30 days. Treated soil was prepared by keeping about 100 ants in the closed container during the waiting period. Potential

contaminants from material were avoided by not feeding the ants during this time. The ants survived the fasting period. Control soil was kept ant free.

The test chamber was a plastic box (length 170 mm, width 110 mm, height 60 mm) filled to a depth of 15 mm with control soil. Two watch glasses (inner diameter 50 mm, inner height 7 mm; outer diameter 65 mm, outer height 15 mm) were placed 10 mm apart (measured from nearest edges) in the centre of the box. The watch glasses were filled with soil, then embedded in the surrounding soil (soil level with the rim of the watch glass). To facilitate seeing whether test spiders were in the watch glass, the rim of each glass was kept clear of soil. Treated soil was placed in the experimental watch glass (ants removed immediately beforehand) and control soil was placed in the control watch glass. Whether treated soil was on the left or right was decided at random for each test. To start a test, a spider was placed on the soil between the two watch glasses. For the next 60 min, we recorded how much time the test spider spent in each watch glass. Time spent outside the watch glasses was ignored.

Effect of chemical cues in soil on behaviour and posture.-- Control and treated soils were prepared as in the experiment on choice of soil. Each test spider was tested on one day with treated soil and on the previous or next day (order decided at random) with control soil. During 15-min tests, the test spider's behaviour was recorded in detail, but we present data here for only those behaviours where there was statistical evidence of behaviour being influenced by soil treatment.

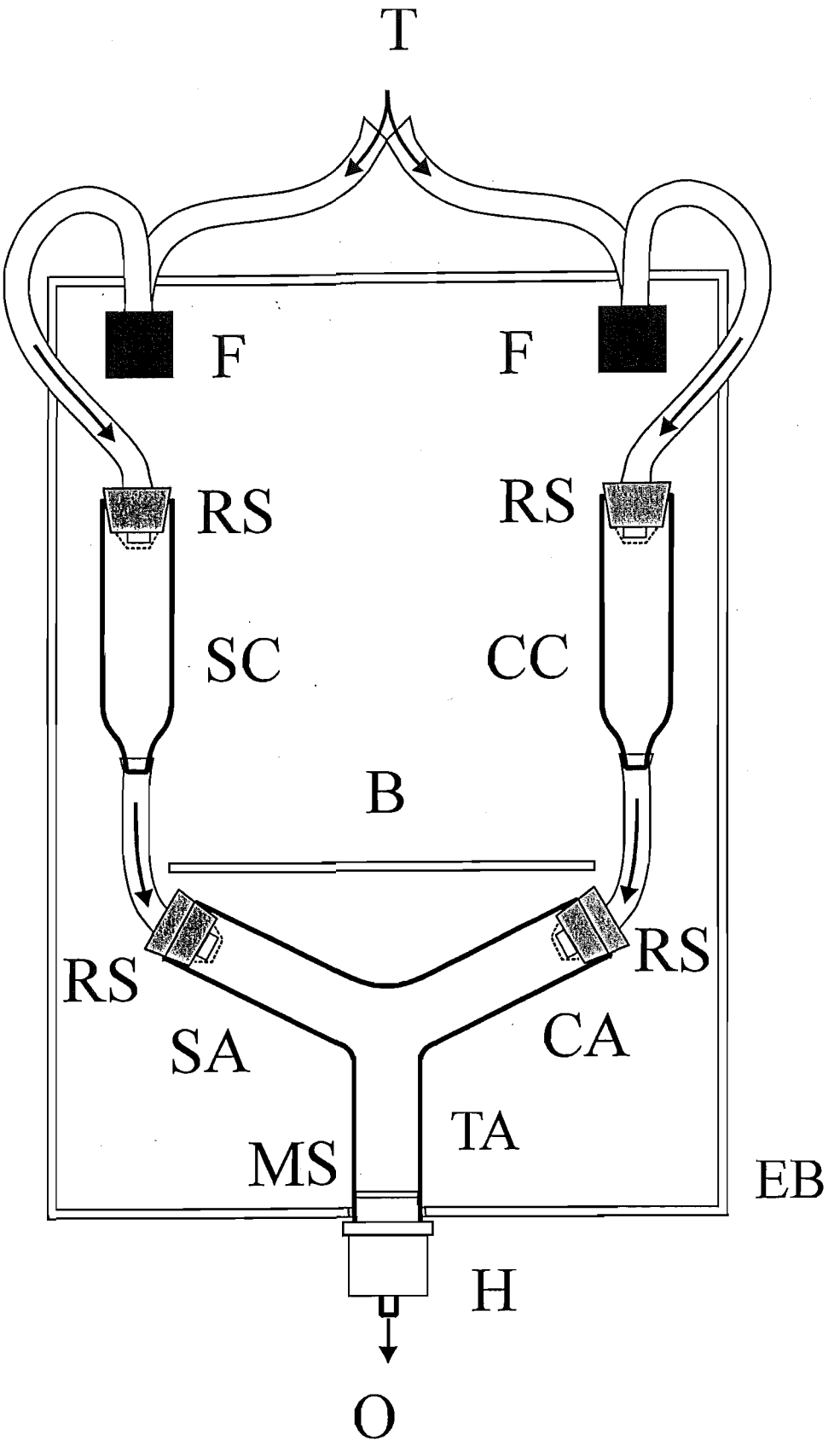
The test chamber was a cylindrical plastic dish (diameter 90 mm, height 40 mm) with soil covering the bottom to a depth of 10 mm. Four corks (diameter 9 mm at the narrow end) were embedded with the upper 5 mm of cork (narrow end) extending above the soil. Corks were evenly spaced in a square centred in the middle of the dish (centre of each cork 20 mm from the centre of the nearest neighbouring cork). Evenly spread around the dish between the corks were four convex 10 x 10 mm pieces of oak leaf (Quercus spp Linnaeaus), each positioned so that the test spider

could walk under it.

Effect of chemical cues in soil on attention to optical cues.-- We investigated whether H. pulex's attention to optical cues from ants is affected by the presence of chemical cues from ants. Preparation of soil and the test chamber was as described for the experiment on how chemical cues affect behaviour and posture, except that no leaf litter was present and there was a glass vial (65 mm long, inner diameter 10 mm) containing two ants on the soil centred between the corks. Latencies to initiate and complete stalking sequences directed at the ants were recorded. Stalking was initiated when the test spider turned toward an ant and began to move steadily toward it, and completed when the test spider touched the vial. Test spiders were allowed 15 min to begin stalking and subsequently allowed 15 min to complete the stalking sequence.

Olfactometer tests.-- A Y-shaped olfactometer (Fig. 1) with airflow adjusted to 1000 ml/min (Matheson FM-1000 flowmeter) was used to assess H. pulex's response to airborne odours from ants. At this airflow setting, there was no evidence that H. pulex's locomotion was impaired. Air flowed from a tap through two separate flowmeters into a stimulus chamber (which contained an odour source) and a control chamber (which was empty). During experimentation, whether the experimental chamber was on the left or right side of the olfactometer was decided at random. Air moved from the stimulus chamber to the stimulus arm and from the control chamber to the control arm. Collectively, the stimulus and control arms are referred to as the "choice arms". Air flowed from the each choice arm into a single test arm. At one end of the test arm, there was a holding chamber into which a spider was placed prior to testing. A metal barrier, positioned in a slit between the holding chamber and the test arm, blocked the spider's entry into the test arm. Thirty minutes before each test, an odour source (depending on the experiment, either four ants or 10 µl of 6-methyl-5-hepten-2-one) was placed in the experimental chamber. This 30-min period allowed the air to circulate evenly and ensured that air pressure was comparable throughout the olfactometer.

Fig. 1. Olfactometer. Arrows indicate direction of airflow. SC: stimulus chamber (contains odour source). CC: control chamber (empty). H: holding chamber (location of test spider at start of test). TA: test arm. CA: control arm. SA: stimulus arm. MS: metal screen fitted in slit (blocks spider's entry into test arm before test begins). T: tap from which air enters olfactometer. B: opaque barrier (prevents test spider from seeing ants). RS: rubber stopper. O: air leaves olfactometer. EB: edge of box enclosing olfactometer. Diagram not to scale. See text for details.


T
F
F
RS
RS
SC
CC
B
RS
RS
SA
CA
TA
MS
EB
H
O

During testing, spiders tended to walk about actively in the olfactometer, sometimes entering the experimental or control arm, or both, several times but staying only briefly. For each spider, we recorded both the first and final choice. The first arm the spider entered was its first choice regardless of how long it stayed. By definition, a spider made its final choice when it entered an arm and remained there for a minimum of 30 sec. A maximum of 60 min was allowed for the spider to make a final choice after leaving the holding chamber. Between tests, the olfactometer was dismantled and cleaned first with 80% ethanol and then with water. This was a precaution against the possibility that spiders might be affected by draglines or chemical traces from previously tested spiders.

RESULTS

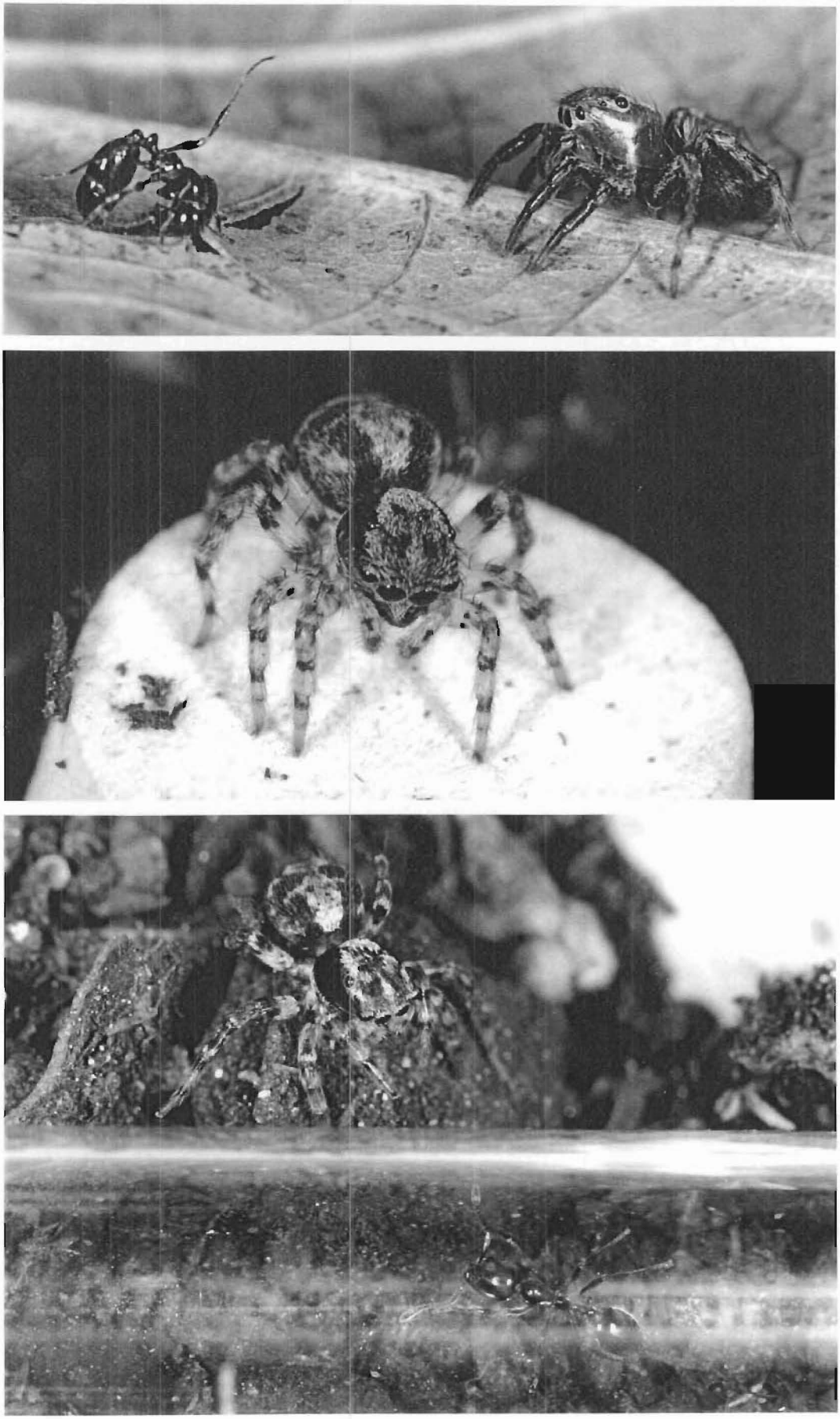
Predation on ants in a complex environment.-- Habrocestum pulex tended to leap on fruit flies from any orientation, but attacked ants by repeatedly approaching head on, making stabs with its fangs, then backing away (Fig. 2). Once the ant was more or less quiescent, H. pulex approached slowly, grasped the ant and began feeding. During and immediately prior to attacking an ant, the spider's palps were retracted to the sides of the chelicerae, but palps tended not to be retracted during attacks on flies.

Locomotion, when it occurred, during tests with flies, tended to be by slow, continuous stepping. The normal posture was adopted with the body ca. 1 mm above the substrate and legs only moderately extended. With ants, prey-capture sequences were normally preceded by distinctive preliminary behaviour which included agitated walking, undirected leaping and posturing with the body elevated. These sequences were often preceded by periods during which H. pulex simply watched (maintained orientation towards) an ant. Agitated walking was a distinctive style of motion

Fig. 2. Habrocestum pulex (on right) slowly approaches ant (Monomorium antarticum) (on left). Ant now quiescent having been repeatedly stabbed by H. pulex.

Fig. 3. Habrocestum pulex on top of cork watching ant (not in photograph) moving about on soil.

Fig. 4. Habrocestum pulex completes stalking sequence in tests of effect of chemical cues in soil on attention to optical cues (see text). H. pulex (above, right) faces ant (glass vial, lower right) and touches glass.



in which H. pulex repeatedly spurted forward for ca. 0.5 sec at 30-50 mm/sec., paused and then spurted forward again. Habrocestum pulex made undirected leaps by suddenly propelling itself more or less straight upward with no target being evident. When in the body-elevated posture, H. pulex stood with its legs more extended than normal, so that its body was 2-3 mm off the substrate.

When predation was delayed or failed to occur in tests with flies, H. pulex spent much of the time sheltering under leaf litter, but H. pulex rarely sheltered under leaves in tests with ants. A common preliminary to predation on both ants and flies was for H. pulex to stand on corks and watch prey active on the soil below (Fig. 3). Attacks were often made by rushing down from a cork, after which H. pulex usually returned to the top of the same cork to feed.

Choice tests using blotting paper.-- Scores were spread more or less evenly over the range of possible values, providing no evidence that H. pulex discriminated between treated and control blotting paper (Fig. 5).

Choice tests using soil.-- H. pulex spent more time on treated, rather than control, soil (Fig. 6). In 20 tests, one spider spent more time on control soil, one spent equal time on treated and control soil, and the remaining 18 spent more time on treated soil (binomial test comparing the number that spent more time on treated versus control soil; $P<0.001$, $N=19$).

Effect of chemical cues in soil on behaviour and posture.-- Agitated walking, undirected leaping, the body-elevated posture, and perching on corks were more prevalent when H. pulex was in experimental chambers rather than control chambers (Table 1).

Effect of chemical cues in soil on attention to optical cues.-- When on treated soil, H. pulex initiated and completed (Fig. 4) stalking sequences against ants more often than when on control soil (Table 1). The latency to initiate and to complete stalking was shorter on treated than control soil (Fig. 7).

Olfactometer tests.-- When tested with ants in the stimulus chamber, the first choice was the

Table 1. Results from experiments on effects of chemical cues in soil on Habrocestum pulex. A) Behavior and posture. B) Attention to optical cues. Each spider tested one day on treated soil (had been in contact with ants) and on alternate day on control soil (had not been in contact with ants). Compared to when on control soil, H. pulex on treated soil: A) performed more agitated walking, undirected leaping, holding body raised and perching on walk; B) initiated and completed stalking. See text for details. Data analysis: McNemar test for significance of changes (for these tests, only the first two columns of data are used).

Experiment	Response	On treated soil only	On control soil only	On both types of soil	On neither type of soil	McNemar test
A)	Agitated walking	8	1	9	2	$P < 0.05$
	Undirected leaping	12	1	2	4	$P < 0.01$
	Holding body raised	12	0	4	4	$P < 0.01$
	Perching on cork	11	1	5	3	$P < 0.01$
B)	Initiate stalking	11	1	7	1	$P < 0.01$
	Complete stalking	12	2	4	2	$P < 0.01$

Fig. 5. Distribution of difference scores (time spent on treated blotting paper minus time spent on control blotting paper) from experiment on choice of blotting paper. See text and Fig. 1 (data more or less evenly spread).. No statistical evidence of preference (Wilcoxon test for paired comparisons, NS).

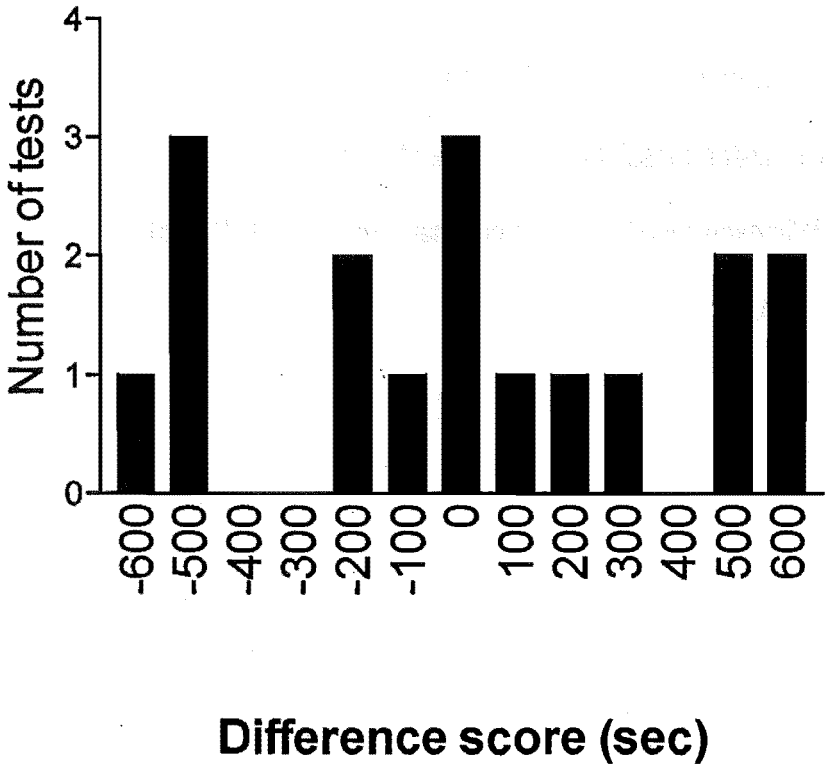

Number of tests
0
1
2
3
4
-600
-500
-400
-300
-200
-100
0
100
200
300
400
500
600
Difference score (sec)

Fig. 6. Distribution of difference scores (time spent in experimental watch glass minus time spent in control watch glass) from experiment on choice of soil, showing preference for treated soil (Wilcoxon test for paired comparisons, $P<0.001$). Note: there was only one negative score. See text and Fig. 2.

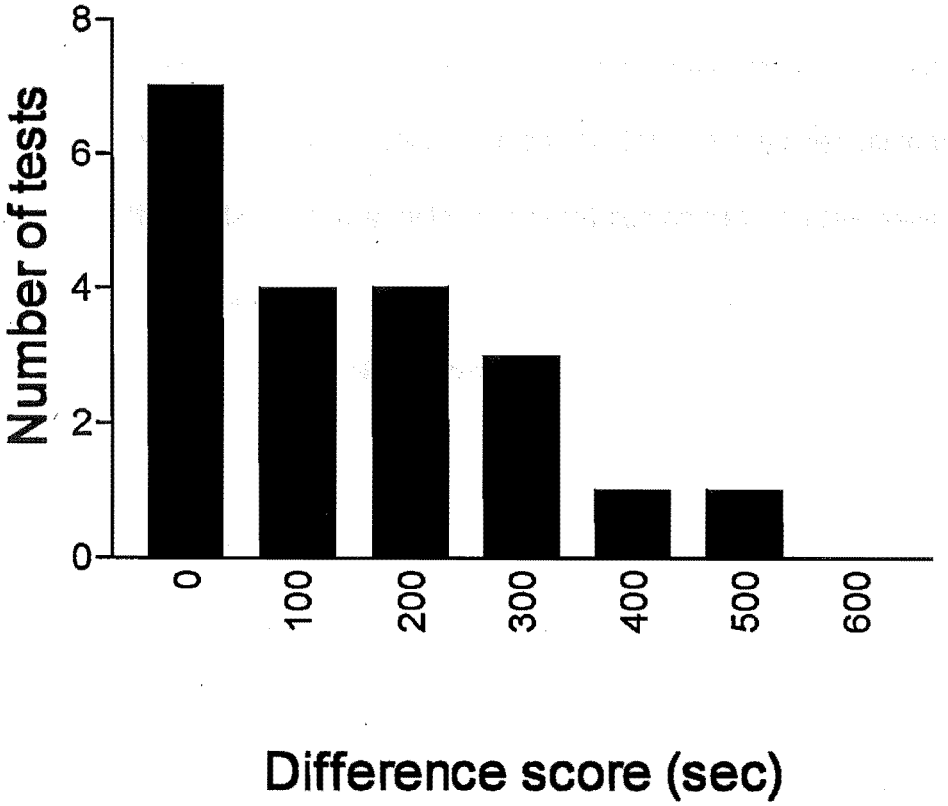
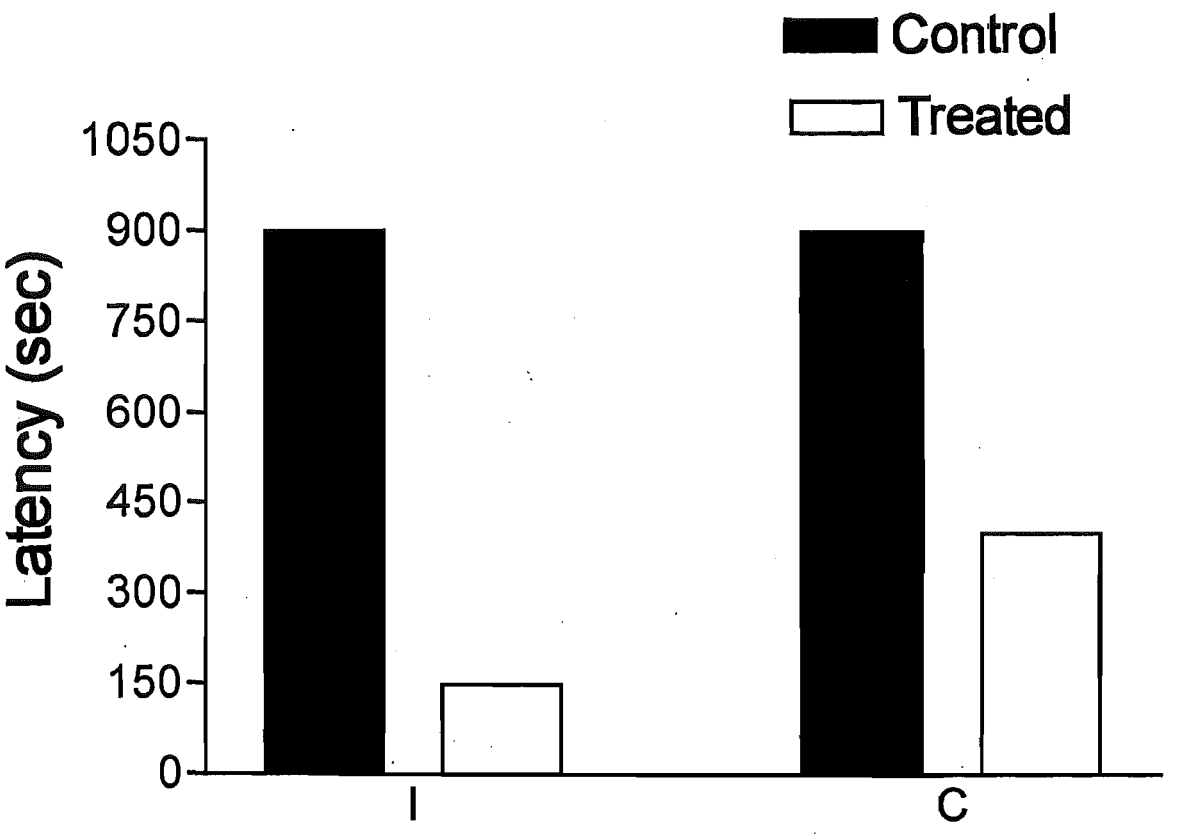

Number of tests
8
6
4
2
0
0
100
200
300
400
500
600
Difference score (sec)

Fig. 7. Latencies to initiate and complete stalking sequence (see text for definitions) in experiment testing for effect of chemical cues in soil on attention to optical cues. Latencies when on treated soil (been in contact with ants) shorter than latencies when on control (clean) soil (Wilcoxon tests for paired comparisons, $P<0.005$ for both initiating and completing stalking). See text and Fig. 4.


Control
Treated
Latency (sec)
1050
900
750
600
450
300
150
0
I
C

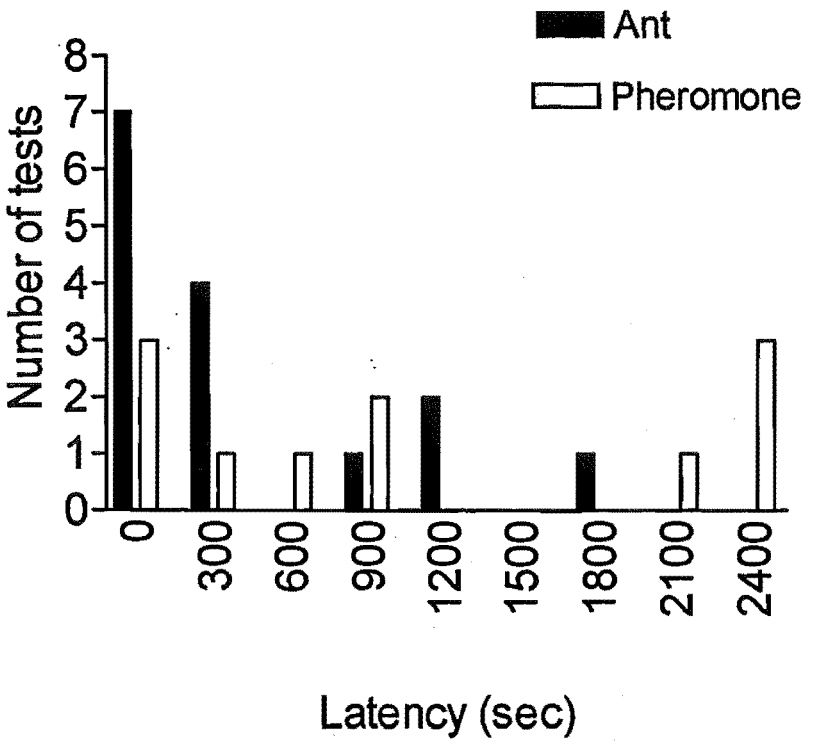
stimulus arm in 11 tests and the control arm in four tests (binomial, $P<0.05$). The final choice was the stimulus arm in 13 tests and control arm in two tests (binomial, $P<0.001$). In all tests in which the stimulus arm contained 6-methyl-5-hepten-2-one, the first and final choice were identical: the stimulus arm in 10 tests and the control arm in one test (binomial, $P<0.001$). There was no statistical evidence of a relationship between the arm chosen and the latency to choose (Mann-Whitney rank-sum test, NS; Fig. 8).

DISCUSSION

Habrocestum pulex apparently detects and responds adaptively to chemical cues from ants. Our findings support the following hypotheses: (1) H. pulex chooses to remain on soil containing chemical cues from ants (choice of soil); (2) ant-derived chemical cues in soil stimulate H. pulex to adopt posture and behaviour appropriate for capturing ants, even in the absence of optical cues from ants (effect of chemical cues on behaviour and posture); (3) ant-derived chemical cues in soil heighten H. pulex's attention to optical cues from ants (effect of chemical cues in soil on attention to optical cues); and (4) H. pulex is attracted by olfaction to chemical cues from ants (olfactometer tests). Failure to show a preference for treated over control blotting paper in a petri dish suggests that blotting-paper choice tests are excessively artificial.

Rather than demonstrating responses to the particular ant species on which H. pulex preys most often in nature, our results suggest that H. pulex has evolved ability to detect and respond adaptively to chemicals secreted by a broader range of ants. In all experiments, we used Monomorium antarcticum, a New Zealand myrmicine ant which would not be encountered by H. pulex in nature. H. pulex preys especially often in nature on Lasius spp. which are formicines. In our experiments, H. pulex was also influenced by 6-methyl-5-hepten-2-one, a ketone characteristic of

Fig. 8. Data from olfactometer experiment. Latency to choose between experimental arm (contained either live ants ("ant"; N=15) or 6-Methyl-5-Hepten-2-one ("pheromone"; N=11)).


Ant
Pheromone
Number of tests
0
1
2
3
4
5
6
7
8
0
300
600
900
1200
1500
1800
2100
2400
Latency (sec)

the mandibular gland secretions of many formicine ants and the anal gland secretions of dolichoderine ants (Duffield et al., 1977). In ants, use of chemically similar pheromones by different species is common (Gabba & Pavan, 1970).

The ketone 6-methyl-5-hepten-2-one appears to be a kairomone not only for H. pulex but also for Habronestes bradleyi Walckenaer, a myrmecophagic zodariid spider. When tested in a Y-shaped olfactometer with a choice between chemical cues from disturbed dolichoderine ants (Iridomyrmex purpureus Smith) and clean air, Habronestes bradleyi most often moved toward the cues from disturbed ants (Allan et al., 1996). Gas chromatography revealed that 6-methyl-5-hepten-2-one is released in high concentrations by injured or disturbed I. purpureus. When retested in the Y-shaped olfactometer, test spiders moved into olfactometer arms which contained 6-methyl-5-hepten-2-one more often than into the clean arms (Allan et al., 1996), implying that this ketone is at least one of the chemicals used by Habronestes bradleyi to locate I. purpureus.

Detecting 6-methyl-5-hepten-2-one is unlikely to be how H. pulex detects M. antarcticum. Whether M. antarcticum uses alarm pheromones is unknown. Other myrmicine ants are known to do so, but they use another closely related ketone, 4-methyl-3-heptanone (Gabba & Pavan, 1970; Hölldobler & Wilson, 1990), instead of 6-methyl-5-hepten-2-one. It may be that, for myrmecophagic spiders, and for ants, sensory systems are not narrowly tuned to particular ketones, but instead respond to a range of structurally related chemicals. Türker (1997a, b) found a correlation between topological indices (which measure structural relatedness) of chemicals and the intensity with which ants respond to them. For example, Pogonomyrmex badius Latreille responds strongly not only to 4-methyl-3-heptanone, its normal alarm pheromone, but also to three structurally related compounds (4-methyl-3 hexane, 3-hexane, and 3-methyl-4 heptanone). Perhaps, H. pulex has evolved chemoreceptors sensitive to a series of structurally related chemicals, rather than those secreted by any particular set of ant species. Broad-sensitivity sensors would

assist H. pulex in predatory sequences against a wide range of ant species, including even New Zealand ants it would never encounter in nature.

Kairomone detection appears to function not only to bring H. pulex into proximity with its prey, but also to elicit changes in behaviour, body posture and locomotion that prepare H. pulex for predation on ants before an ant is seen. In particular, cues from ants caused H. pulex to move to higher ground (i.e., perch on corks), where its ability to detect optical cues from ants might be enhanced, and H. pulex often launched attacks on ants from elevated positions.

Habrocestum pulex illustrates that the evolution of complex eyes and exceptionally intricate vision-based predatory behaviour in salticids is not incompatible with refined kairomone-detection abilities and intricate chemical-mediated predatory behaviour in myrmecophagic salticids. In salticids, a vision-based perceptual and behaviour system appears to have only minimal, if any, cost to proficiency at using a chemical -based perceptual and behaviour system (Jackson & Pollard, 1996, 1997). In H. pulex, the ways in which chemoreception influences predatory behaviour are as intricate as those known for any non-salticid spider. Independently of optical cues, H. pulex not only appears to use kairomones for locating and preparing to prey on ants. Kairomones also appear to influence attention to optical cues. When ant-derived cues were present, H. pulex located ants faster than when they were absent. This suggests that the chemical and vision-based perceptual systems of salticids may have reached a remarkable level of integration.

CHAPTER 7:

REACTIONS OF HABROCESTUM PULEX, A MYRMECOPHAGIC SALTICID, TO POTENTIAL KAIROMONES FROM ANTS

ABSTRACT

Experiments were conducted to determine whether responses by Habrocestum pulex to chemical cues from ants (see Chapter 6) were: (1) specific to ants or generalised responses to a wider set of potential prey; (2) cued predatory responses or stress-induced responses to aversive stimuli. In choice tests there was no statistical evidence that Habrocestum pulex discriminated between formic-acid coated and clean blotting paper. The behaviour and posture of Habrocestum pulex was observed in formic-acid-treated, fly-treated, ant-treated and clean cages. That cues from live ants and formic acid influenced behaviour was suggested, but there was no discernible difference in the behaviour of Habrocestum pulex when in ant and formic-acid-treated cages. That fly-treated cages influenced Habrocestum pulex is also suggested. There was no statistical evidence that the behaviour of the other salticids tested (Portia africana, Portia fimbriata and Trite planiceps) were influenced by substrate. Habrocestum pulex, when tested with lures made from ants, retracted its palps and began stalking more often in clean cages than in ant-treated cages. In contrast, Habrocestum pulex more often made undirected leaps and adopted lowered palps and body elevated postures in ant-treated cages than in clean cages.

INTRODUCTION

Most salticids tend to exclude ants from their diets, but for a minority ("myrmecophagic" salticids) ants are preferred prey. Earlier studies have shown that optical cues alone are sufficient to

elicit ant-specific prey-capture behaviour (e.g., Li et al., 1997) in myrmecophagic salticids, the potential role of chemical cues in stimulating ant-specific capture behaviour is less clearly understood. In Chapter 4, Habrocestum pulex (Hentz) was shown to: (1) remain in areas where ant-derived chemical cues were present; (2) change behaviour in ways that facilitated the capture of ants; (3) heighten attention to optical cues from ants. These findings were interpreted as evidence that H. pulex uses ant-derived kairomones (chemicals emitted by one animal, but detected by individuals of another species, that provoke a response favourable to the detector but not the sender of the cue; Brown et al., 1971). The current chapter is a closer examination of this conclusion. I investigate two questions: (1) are the previously demonstrated responses of H. pulex to ants specific to ants or generalised responses to all potential prey; and (2) are they cued predatory responses to the presence of prey, or are they instead negative responses to aversive stimuli?

The first question is investigated by comparing H. pulex's response to chemical cues from ants and from houseflies (Musca domestica (Linnaeus)). The second question is investigated by comparing H. pulex's response to ant-derived chemical cues with response by three non-myrmecophagic salticids to the same cues.

Ants make extensive use of chemicals both as pheromones functioning in intraspecific communication and as anti-predator deterrents (Hölldobler & Wilson, 1990). These same chemicals are potentially kairomones available to predators that might intercept them and use them to find the ant. Whether myrmecophagic salticids use kairomones from ants has rarely been considered, the most detailed study to date being Allan et al. (1996) who showed that an ant alarm pheromone is used as a kairomone by an ant-eating zodariid spider.

In the present study, I investigate whether formic acid is used by myrmecophagic salticids as a kairomone. Formic acid, first distilled from wood ants 300 years ago (Wray, 1670), may be the best known example of a chemical used by ants for anti-predator defence. However, formic acid is only one of the numerous anti-predator deterrents used by ants (Blum, 1992), and its use is

restricted to one large subfamily, the Formicinae.

All myrmecophagic salticids that have been studied in detail prey on a wide range of ants, including not only formicine ants but also ants from other families. Adopting formic acid as a kairomone, although not sufficient for detection of all ants preyed upon, might be frequently advantageous for myrmecophagic salticids. Following an attack by one predator on an ant, traces of formic acid may be left in the environment, potentially informing the salticid of the presence of ants, even after the initial predator, the alarmed ant or both have departed.

Although disturbed ants secrete highly concentrated formic acid (40-60%; Stumper, 1951,; Osman & Brander, 1961; Blum, 1992), concentration tends to decrease by the inverse square law with the distance away from its source. Ant predators, such as myrmecophagic spiders, despite being repelled by high concentrations of formic acid, might react positively to trace amounts of formic acid. Low concentrations of formic acid might warn a salticid that ants are nearby and allow the predator to better prepare for attacking ants not yet seen. Conversely, non-myrmecophagic predators might benefit from detection of environmental traces of formic acid. For these species, the expected response might be to move away, thus diminishing the likelihood of a dangerous encounter with ants. More complex responses might also be found.

GENERAL METHODS

Except for minor modifications, maintenance procedures, cage design and data analysis were as in earlier studies (Jackson & Hallas, 1986a). Experiments using H. pulex, were carried out in New Zealand, using laboratory cultures derived from ants originally collected in Kansas, U.S.A.

In observations and experiments with live ants, I used Monomorium antarcticum Smith, a myrmicine ant native to New Zealand (Ettershank, 1966; Bolton, 1987). Instead of formic acid, the

primary chemical defence of this species is an alkaloid-based venom (Jones et al., 1988).

Adult females of three species of non-myrmecophagic salticids were used: Portia fimbriata (Doleschall), P. schultzi, and Trite planiceps Urquhart. P. schultzi (Simon) and P. fimbriata prefer other spiders as prey and actively avoid coming into contact with ants (Li & Jackson, 1996b; Li et al., 1997; Jackson et al., unpub. data). T. planiceps, is a more or less typical insectivorous salticid that normally rejects ants as prey (Jackson & van Olphen, 1991; Jackson, pers. obs.).

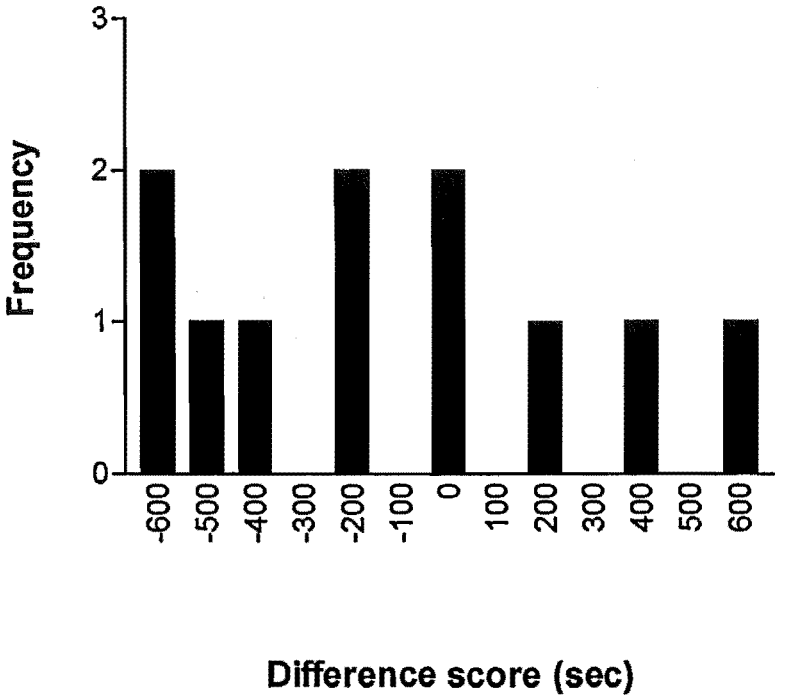
Each individual salticid was used in a maximum of two tests for any one experiment and there was no evidence that the identity of individual salticids influenced test outcome. Data from H. pulex from males and females, not being statistically different, were pooled. Statistical methods were from Sokal & Rohlf (1995).

EXPERIMENT 1: CHOICE TESTS USING FORMIC ACID

As a first step in investigating the response of H. pulex to formic acid, I conducted choice tests. The goal was to determine whether H. pulex's movement was affected by formic acid. Choice-test procedure, cage design, and general details concerning maintenance of spiders were as described in Chapter 3. Test spiders were given a choice between spending their time on treated or control blotting paper. Formic acid (2%) had been brushed over the whole surface of treated blotting paper. Control blotting paper was clean.

Results were spread across the range of possible values, providing no statistical evidence that H. pulex discriminated between treated and control blotting paper (Fig. 1).

Figure 1. Difference scores (time spent on formic- acid-treated blotting paper minus time spent on clean blotting paper) from choice tests (Experiment 1) using Habrocestum pulex. Choice between walking over formic-acid-treated and clean blotting paper. No statistical evidence (Wilcoxon-signed rank test) of discrimination between formic-acid-treated and clean blotting paper.


Frequency
3
2
1
0
-600
-500
-400
-300
-200
-100
0
100
200
300
400
500
600
Difference score (sec)

EXPERIMENT 2. EFFECT OF ANT-DERIVED CHEMICAL CUES ON BEHAVIOUR AND POSTURE OF MYRMECOPHAGIC AND NON-MYRMECOPHAGIC SALTICIDS

Methods

As H. pulex, the myrmecophagic salticid, is smaller than the non-myrmecophagic salticids used, petri dishes (diameter 90 mm) were used as test arenas for H. pulex (body length ca 5 mm), but larger rectangular cages (144 mm X 100 mm; see Fig 1, Jackson & Pollard, 1990) were used for tests with P. fimbriata, P. schultzi and T. planiceps (body length 10-12 mm). Twigs and leaves covered ca 30% of the bottom of the test cage.

Cages were conditioned by releasing four ants (Monomorium antarcticum Smith; body length 4 mm) or two houseflies (Musca domestica; body length 8 mm) inside, then removing them 2 h later. The ants and flies walked about actively during the conditioning period.

Cages treated with formic acid were prepared by brushing 2% formic acid solution over the entire basal surface of the cage, immediately before testing. Excess formic acid was then allowed to evaporate for 5 min, leaving the paper only slightly damp. A salticid ("test spider") was placed in a plastic tube (length 65 mm; internal diameter 10 mm) and the tube was inserted through a hole in the base of the cage. Test spiders were then allowed to leave the tube of their own accord. After a 5-min settling down period, the spider's behaviour was observed over the next 15 min. Control tests were conducted in the same way except that no ants, flies or formic acid had been used to condition the cages.

Following testing, cages were washed with ethanol and water to remove chemical traces remaining from previous trials. No spider was tested more than once for any particular treatment. The behaviour of the spider during each test was recorded in detail. For H. pulex and T. planiceps, only those behaviours that appeared to be influenced by substrate conditioning are described in detail here. Additional behaviours and postures are described fully elsewhere (P. fimbriata, Chapter

3; H. pulex, Chapter 6; T. planiceps, Taylor & Jackson, 1999).

When performing agitated walking, H. pulex moved rapidly (30- 50 mm/sec) in short, frequent spurts. Normal walking was characteristically in a slower (ca 15 mm/sec) and calmer gait. When making undirected leaps, the spider suddenly propelled itself into the air, with no target being evident. Three body postures were also important in H. pulex: body held parallel to and 2-3 mm above the substrate ('body raised'); body held parallel to, and in contact with the substrate ('body lowered'); posterior tip of abdomen touching the substrate and the anterior end of the thorax raised at an angle of 45 degrees to the substrate ('body tilted').

For statistical analysis, H. pulex's behaviour in cages treated with formic acid was compared to its behaviour in ant-treated, fly treated and clean cages (X^2 tests of independence, 4X2 tables). To determine which substrates elicited particular responses, multiple comparisons (2X2 tables; X^2 tests of independence, with Bonferroni adjustment) were conducted whenever initial statistical testing (4X2 tables) indicated that the substrate affected the incidence of the particular behaviour or posture considered.

Results

Several behaviours and postures were adopted by H. pulex more often when on treated substrates than when on control substrates (Table 1): (1) postures with the body tilted ($P<0.001$), raised above the substrate ($P<0.05$), and lowered to the substrate ($P<0.05$); (2) postures with the legs extended ($P<0.01$) and hunched ($P<0.001$); (3) postures with the palps retracted ($P<0.05$); (4) undirected leaping and perching on walls (both $P<0.05$).

There was no statistical evidence that H. pulex's responses to ant-treated cages and formic-acid-treated cages ('ant-derived substances') differed. H. pulex adopted three postures (body tilted, $P<0.05$; legs extended, $P<0.05$; legs hunched, $P<0.01$) more often in ant-treated than when in clean cages. Three behaviours, undirected leaping ($P<0.05$), perching on walls ($P<0.001$) and agitated

Table 1. Data on effect of ant-derived chemicals on behaviour and posture (Expt. 2). Incidence (number of tests occurred; N, total number of tests) of H. pulex's behaviour and postures, in ant-treated, fly-treated, formic-acid treated and control cages.

Behaviour	Occurred on ant-treated substrates	Occurred on fly-treated substrates	Occurred on formic-acid-treated substrates	Occurred on clean substrates (control)	P[1]
N	14	15	13	15	
Calm walk	8	13	11	8	N.S.
Agitated walk	13	8	8	5	0.05
Undirected leaping	11	6	11	5	0.01
Leg extended	13	14	12	8	0.01
Leg hunched	13	7	13	5	0.001
Retracted palps	12	12	12	7	0.05
Extended palps	13	10	12	10	N.S.
Body tilted	13	15	13	9	0.005
Body lowered	7	5	7	1	N.S.
Body raised	13	11	12	7	0.05
Perched on wall	12	3	10	6	0.001

[1] Significance level (X^2 test of independence, 4X2 table) from comparing incidence of behaviour and postures of H. pulex, when in cages with 2% formic acid solution, cages previously occupied by flies or myrmicine ants, or clean cages.

walking ($P<0.05$), occurred more often when H. pulex was in ant-treated cages, than when in clean cages. H. pulex made undirected leaps ($P<0.05$), perched on walls ($P<0.05$) and performed agitated walking ($P<0.05$), more often when in ant-treated than in fly-treated cages.

Three body postures (body tilted, $P<0.05$; legs hunched, $P<0.01$; legs extended, $P<0.05$) and two behaviours occurred in formic-acid treated more often than control cages. H. pulex perched on walls ($P<0.01$), made undirected leaps ($P<0.05$) and adopted postures with the legs hunched ($P<0.01$) more often when in formic-acid treated than in fly-treated cages.

The incidence of most behaviours and postures of H. pulex was the same in fly-treated or control cages. However, H. pulex adopted postures with the legs extended or body tilted more often in fly-treated than in clean cages ($P<0.05$ for both).

In contrast to H. pulex, there was no statistical evidence that the incidence of behaviours and postures of P. schultzi, Portia fimbriata (Table 2) and Trite planiceps (Table 3) were influenced by substrate.

EXPERIMENT 3. EFFECTS OF CHEMICAL CUES FROM LURES ON HABROCESTUM PULEX'S ATTENTION TO OPTICAL CUES FROM PREY

Methods

Details of the test arena layout were as described in Chapter 3 (Experiment 2). In each test, a lure was present, always centred 40 mm from one end of the cage and oriented so that it faced the opposite end of the cage. Ants used for lures were first immobilised under carbon dioxide, then preserved in 80% ethanol. A lure was made by removing the ant, letting it dry, then mounting it on a disc-shaped piece of cork (diameter c 10 mm). The mounted dead ant and the cork were sprayed with an aerosol plastic adhesive (crystal clear lacquer, Atsco Australia Pty) for preservation and to mask chemical cues that might have remained on the dead spider. During testing, the chamber (see

Table 2. Data on effect of ant-derived chemicals on behaviour and posture (Expt. 2). Incidence (number of tests occurred; N, total number of tests) of behaviours and postures of two species of Portia, when in ant-treated or control (clean) cages. No statistical evidence that test spiders behaviour was affected by substrate (X^2 test of independence).

Behaviour	P. schultzi on ant-treated substrates	P. schultzi on clean substrates	P. fimbriata on ant-treated substrates	P. fimbriata on clean substrates
N	25	22	8	6
Extended leg position	19	13	7	4
Hunched legs	18	12	8	6
Huddled leg position	19	13	0	0
Normal palps	8	10	6	3
Lateral palps	23	17	6	6
Tap with palps	19	9	6	2
Body tilted	17	18	8	5
Body lowered	10	13	8	5
Body raised	10	13	2	2
Creeping	1	1	0	0
Normal walking	14	17	5	2
Mechanical walking	8	4	3	2
Undirected leaps	0	1	0	1
Perch on wall	14	16	6	2
Perch on roof	0	0	5	1

Table 3. Data on effect of ant-derived chemicals on behaviour and posture (Expt. 2). Incidence (number of tests occurred; N, total number of tests) of behaviours and postures of Trite planiceps, when ant-treated or clean cages. No statistical evidence that T. planiceps's behaviour was affected by substrate (X^2 test of independence).

Behaviour	T. planiceps on ant-treated Substrates	T. planiceps on clean substrates
N	11	12
Calm walk	9	5
Agitated walk	4	7
Darting walk	4	4
Reversed walk	4	1
Abdomen arched	6	6
Abdomen straight	8	8
Abdomen substrate	10	9
Palps beside body	10	10
Palps substrate	9	11
Palps outstretched	1	3
Legs crouched	11	10
Legs outstretched	7	6
Front legs extended	9	8
Perched on stick	2	2
Perched on leaf	5	2
Perched on wall	10	8
Undirected leaping	2	0
Hide under leaf	2	2

Chapter 3) was inclined at c. 20°, with the lure at the raised end. To start a test, a spider was introduced at the opposite end. Spiders tended to walk upward in the chamber, thereby getting closer to the lure.

Stalking was a distinctive behaviour in which spiders moved directly and steadily toward lures. We recorded whether test spiders began to stalk (turned toward lure and walked more or less directly toward it) and whether they got close (within 15 mm) to the lure. During testing, the incidence of other behaviours and postures was also recorded. Tests ended once H. pulex stalked close to the lure or 1 h elapsed. Descriptions of behaviours and postures are as in Experiment 1, except that an additional posture was important: palps parallel to the chelicerae, but held near to the substrate ("lowered palps").

Results

There was no statistical evidence that the tendency to begin stalking or to stalk until close to lures was affected by substrate (Table 4). Compared to when in clean cages, H. pulex was more prone when in ant-treated cages to adopt postures with palps lowered ($P<0.05$; Table 4).

DISCUSSION

Previous studies (Li et al., 1996) have shown that optical cues from ants are sufficient to stimulate H. pulex to begin ant-specific prey-capture behaviour. In the present study, Experiment 2 showed that chemical cues from ants, in the absence of visual cues, stimulate H. pulex to begin prey-capture behaviour. Three behavioural responses (agitated walking, undirected leaping, and

Table 4. Data on effect of chemical and visual cues from lures on Habrocestum pulex's attention (Expt. 2). Incidence (number of tests occurred) of behaviours and postures of H. pulex, when in ant-treated or clean (control) cages. During testing a lure, made from a preserved ant (Monomorium antarticum) was present in the cage. H. pulex was tested on ant-treated and clean substrates on alternate days (11 tests for each treatment, order random).

Behaviour	Occurred in ant-treated cages only	Occurred in clean cages only	Occurred in both types of cage	Occurred in neither type of cage	P[1]
Began to approach lure	1	6	1	3	N.S.
Stalked close to lure	1	1	0	9	N.S.
Agitated walk	4	1	2	4	N.S.
Calm walk	2	3	5	1	N.S.
Undirected leaping	3	0	3	5	N.S.
Extended leg position	4	3	2	2	N.S.
Hunched leg position	2	5	3	1	N.S.
Retracted palps	0	3	6	2	N.S.
Lowered palps	4	0	3	4	0.05
Body tilted	3	3	4	1	N.S.
Lowered body	1	1	1	8	N.S.
Raised body	3	0	6	2	N.S.
Perch on wall	5	1	2	3	N.S.

[1] P-value for McNemar test for significance of changes.

perching on walls) seem to be specific to ants. However, these responses are not specific to the ants on which H. pulex preys in nature, as Monomorium antarcticum, an ant endemic to New Zealand, was used for these experiments. H. pulex appears to have generalised sensitivity to a wide spectrum of ant-derived chemical cues (see Chapter 6).

H. pulex, an ant predator, appears to prepare for prey-capture behaviour after encountering ant-derived chemical cues, but the expected response by non-myrmecophagic salticids to ant-derived chemical cues would be avoidance behaviour. My results were not consistent with this hypothesis, as there was no evidence that the non-myrmecophagic salticids tested responded to chemical cues from ants at all. However, the use of different cage sizes may complicate interpretation, and this experiment should be repeated using smaller non-myrmecophagic salticids in petri dishes.

Earlier experiments (Chapter 6) showed that H. pulex tends to: (1) remain in areas where ant-derived chemical cues are present; (2) change behaviour in ways that facilitate the capture of ants; (3) heighten attention to optical cues from ants. Results in the present chapter are not consistent with these earlier findings: (1) when in ant-treated cages, H. pulex was less likely to approach ant-lures than in clean cages; and (2) there was no evident tendency to remain in areas with ant-derived chemicals. Two differences in methodology may explain these inconsistencies. In Chapter 6 live ants were used (in contrast to lures) and tests were conducted in cages with soil present.

Previous experiments (Li et al., 1996) showed that H. pulex responds to immobile lures made from ants, but this does not rule out the possibility that movement is also an important cue mediating predatory behaviour. It may be that H. pulex often fails to interpret an immobile ant as either a threat or a potential meal. Chemical cues elicited heightened attention to cues from mobile ants (Chapter 6), but not to immobile ants (current chapter). As ants are usually active when encountered, reliance on movement cues may not be surprising. Perhaps when encountering ant-

derived chemical cues, H. pulex becomes more cautious until moving ants are discovered. It may be that H. pulex's optimal response upon encountering ant-derived chemical cues is to look from a distance for moving ants, rather than to move into areas where ant-derived chemical cues are in high concentration. This might minimise the risk of being attacked by an unseen ant, and it may also explain the apparent lack of discrimination between formic-acid-coated and clean blotting paper during the choice tests.

The apparent importance of movement by ants is consistent with an earlier study (Depree, 1992), an unpublished M.Sc. thesis. Depree's findings suggest that optical cues from ants may be important in mediating how a non-myrmecophagic salticid reacts to ants. Two experiments were conducted: (1) ants inside glass tube coated with a 10% solution of formic acid; (2) fruit flies (Drosophila melanogaster Meigen) inside glass tube coated with a 10% solution of formic acid. There were control tests conducted using both types of insect, but no formic acid. During testing, a non-myrmecophagic salticid, Euophrys parvula Bryant, was introduced into the cage to see whether it attempted to attack the insects in the tube. E. parvula attacked ants 20% of the time when no formic acid was on the outside of the tube, but never attacked when formic acid was present. Test spiders attempted to attack fruit flies in formic-acid-coated tubes in only half of the tests, compared with 80% of the tests when no formic acid was present. These results suggest that 10% formic acid has an aversive effect, but it seems that optical cues from ants are also important, as E. parvula seemed to be avoiding ants rather than formic acid. That is, for low concentrations of formic acid, optical cues from ants may be more important in mediating avoidance of formicine ants than formic acid.

The importance of soil, which was used in Chapter 6, but not the present chapter, needs to be clarified. It may be that the cue is absorbed by soil but not plastic, resulting in the time critical chemicals are available for detection being longer on soil than on plastic. H. pulex changed its behaviour in cages when chemical cues from ants were present, suggesting that ant-revealing

chemical cues were available (in the absence of soil) for detection by H. pulex. However, the concentration of these cues may not have been high enough to elicit changes in H. pulex's attention to optical cues. Experiments should be undertaken using immobile lures in conjunction with soil or using moving lures in cages without soil. Unfortunately, our cultures of H. pulex died out before these tests could be attempted.

CHAPTER 8:

DRAGLINES AND ASSESSMENT OF FIGHTING ABILITY IN CANNIBALISTIC JUMPING SPIDERS

ABSTRACT

The frequency of injury and death during female-female aggression varies in the jumping spider genus *Portia*, with interactions being more violent (likely to end in death or injury of one of the combatants) in *P. labiata* (from Sri Lanka) than in another two species (*P. fimbriata* from Australia and *P. schultzi* from Kenya). To investigate the role of draglines in the assessment of fighting ability, two types of tests were carried out: 1) dragline discrimination and 2) mirror image response (*Portia*'s reaction to mirror images is comparable to interaction with conspecific rivals). For both types of testing, triplets of equal-size conspecific females were used: one female (the 'test spider') was exposed to draglines of two equal-size conspecific females they had not encountered before ('donor spiders'). The fighting abilities of donor spiders were determined directly by staging intraspecific contests between them. In dragline-discrimination tests (spider placed in petri dish containing draglines from two conspecific females with different fighting ability), females of *P. labiata*, but not the other two species, avoided draglines of the superior fighter (i.e., they spent the majority of their time on draglines of donor spiders with lesser fighting ability). For mirror-image testing, the test spider was placed in a petri dish containing a mirror and draglines. Each test spider was tested on two successive days, with donor draglines in the two tests coming from conspecific females with different fighting ability. In these tests, females of *P. labiata* (but not the other two species) spent less time embracing (each spider pressing its forelegs, palps and front of body against

the other spider) and more time in a part of the petri dish where view of the mirror was obstructed when on the draglines of donor spiders with greater fighting ability than when on the other conspecific's draglines. Findings from this study suggest that *P. labiata* females use signpost cues associated with draglines to assess the relative fighting abilities of unknown opponents.

INTRODUCTION

Assessment of the fighting ability of rivals may help account for ritualized displays in many animals (Enquist et al., 1990; Watson, 1990; Waas, 1991; Rubenstein and Hack, 1992), including spiders (Wells, 1988; Jackson and Cooper, 1991; Faber and Baylis, 1994; Jackson and Pollard, 1997). For animals facing potential rivals that have dangerous weapons (e.g., the fangs and venom of spiders) it might be especially advantageous to assess fighting ability and resource holding power (RHP; Parker, 1974) by detecting signposts (cues left in the environment) before a contest begins (see: Hammerstein, 1981; Enquist and Leimar, 1990). However, there are theoretical problems associated with understanding how signposts would be stable against bluffing (Hasson 1994) and, until recently, the possibility of signposts being used in assessment of fighting ability has received little attention.

Signposts are typically envisaged as signals deliberately left behind by the sender (i.e., leaving the signal is envisaged as an adaptation of the sender that functions in communication). The problem with signposts is that they would appear to be easy to cheat on. The other individual, the receiver, can be expected to discriminate against unreliable signals (Hasson, 1994). We expect a link between a signal and the signalling animal's ability or willingness to fight effectively. Otherwise, it would tend to be to the receiver's advantage to ignore the signal (Johnstone, 1997). It is unclear how signposts would be constrained in this

way because the sender is not necessarily present when the receiver, a potential opponent, comes across the message. If the sender is bluffing, then the receiver can not readily call the sender's bluff by initiating an interaction.

Yet, chemical signposts of mice (*Mus musculus*) reveal the dominance status of males (Hurst, 1993; Drickamer, 1992). Red-backed salamanders (*Plethodon cinereus*) also use chemical signposts to discriminate between unfamiliar potential rivals of different sizes (Mathis, 1990; Mathis and Simon, 1994). In the salamander studies (Mathis, 1990; Mathis and Simon, 1994), there was no direct evidence that the larger animal did in fact have greater fighting ability, but size is known to be a reliable indicator of fighting ability in many animals (Huntingford and Turner, 1987).

Another possibility is that the signpost may not actually be a deliberate signal. Instead, the ability of the receiver to gain information from the signpost may be more akin to mind reading than to receiving intended information (Krebs and Dawkins, 1985). Chemical cues passed between conspecific individuals are typically called 'pheromones' (Karlson and Butenandt, 1959), but three terms (allomone, kairomone and synomone) are in common usage for chemical cues received from non-conspecific individuals. Allomones are advantageous to the sender alone, kairomones to the receiver alone, and synomones to both (Gullan and Cranston 1994). Parallel distinctions are relevant to chemical cues that influence interactions between conspecifics (Dusenbery, 1992). The idea of a kairomone is that information is leaked out from the emitter and is intercepted by the receiver. The possibility of leaked information should also be recognised also for chemical cues acting within a single species. If the sender leaks rather than broadcasts information about fighting ability, then the issue of cheating is not so prominent. For leaked information, the question becomes not so much why the sender fails to cheat but why it has been unable to plug the leak.

Abilities to detect signposts that reliably indicate fighting ability may be especially important in *Portia*, a genus of jumping spiders (Salticidae) in which fatal fights are unusually common (Jackson and Pollard, 1997). Unlike most salticids, which are primarily cursorial insectivores (Richman and Jackson, 1991, Jackson and Pollard, 1996), all species of *Portia* studied build webs which serve as defended territories. They leave their webs to hunt for their prey. Spiders are *Portia*'s preferred prey (Li and Jackson, 1996a, 1997; Li et al., 1997), and these prey are captured by web invasion and the use of aggressive-mimicry signalling (Jackson and Blest, 1982a; Jackson, 1992; Jackson and Wilcox, 1998).

Portia females use their webs as brooding sites for their eggs. Rival females sometimes forcefully take over webs, eat the residents' eggs, then use the stolen webs as brooding sites for their own eggs (Jackson and Pollard, 1997). These territorial conflicts may end in the death or injury of one or both of the combatants.

In many spiders (Jackson, 1987; Pollard et al., 1987), including species in the genus *Portia* (Clark and Jackson, 1995a), draglines laid down during normal locomotion reveal the sex and species of the source spider. In addition, females of *P. labiata* distinguish between their own draglines and the draglines of other conspecific females (self recognition: Clark and Jackson, 1994a) and between the draglines of familiar and unfamiliar conspecifics (Clark and Jackson, 1995b), but these abilities appear to be absent in *P. fimbriata* and *P. schultzi.* Experiments with aged and ethanol-washed draglines indicate that sex discrimination is most probably based on chemical cues (Clark and Jackson, 1995a).

In earlier studies, it was suggested that pronounced ability for self and familiar-unfamiliar discrimination in *P. labiata* may be related to the exceptionally violent nature of intraspecific conflicts in this species (Clark and Jackson, 1994a, 1995b): advance warning of the possibility of a fight with another individual may be disproportionately advantageous to this

species. In the present paper we investigate in *Portia* another perceptual ability that would appear to be advantageous: ability to gain advance warning of the relative fighting abilities of potential rivals, independent of prior experience with them.

We investigate the abilities of *P. labiata*, *P. fimbriata* and *P. schultzi* to discriminate between signposts (draglines) of conspecifics with different fighting ability, where we ascertain fighting ability independent of the test spider's response to the draglines. By using for sources of draglines only conspecifics that have never been encountered by the test spider, we rule out confounding effects of prior experience with these potential rivals.

In many animals, there is a tendency for larger individuals to win contests more often than smaller individuals. This trend, if it applies to *Portia* at all, is not pronounced (Jackson, 1982; Jackson & Hallas, 1986a). However, size is not a variable in the present study because we consider only those differences in fighting ability that are independent of size difference.

MATERIALS AND METHODS

General

Standard maintenance procedures in a controlled-environment laboratory, as detailed elsewhere (Jackson and Hallas, 1986a), were adopted in the present study. Cultures of *P. fimbriata*, *P. labiata* and *P. schultzi* originated from Australia, Sri Lanka and Kenya, respectively. We used two methods, dragline-discrimination tests and mirror-image tests, to test how *Portia* females respond to dragline-covered substrates.

In dragline-discrimination tests, the spider was forced to spend its time on draglines of one of two potential rivals. If the test spider can discern from draglines the fighting abilities of unknown rivals, then we predict that the side of the test chamber covered by draglines from the rival with inferior fighting ability will be favoured.

In mirror-image tests, the test spider was allowed to see its own mirror image while standing on the draglines of unknown potential rivals. From earlier studies (Jackson and Blest, 1982b), it is known that *Portia* interacts with its own mirror image by displaying in much the same way as with actual rivals. In addition, we provided a location in the test chamber where the test spider's view of the mirror was obstructed. If the test spider can discern the fighting ability of unknown rivals from draglines, then we predict that, when in the presence of draglines from a rival with superior fighting ability, the test spider will a) spend more time hidden (i.e., in the location where the view of the mirror is obstructed) and b) be less inclined to escalate the intensity of the interaction with the mirror image (i.e., less often progress from displays at a distance to contact with the mirror surface).

Dragline-discrimination tests

For these tests, we modified procedures used in previous dragline-discrimination studies (Clark and Jackson 1994a, 1995a, b). For each test, three adult females of the same species were chosen at random from the laboratory stock, except that the three individuals were matched for body length (within 1 mm) and had not previously interacted with each other. Two of the spiders were selected at random to be dragline donors and combatants, with the third spider being the test spider. To collect draglines, each donor was placed in a different petri dish (diameter 90 mm) which had circular blotting paper taped to the top and bottom. The donor spider was allowed to walk around for 2 h laying down draglines in its petri dish.

Next the two donor spiders were introduced simultaneously into a glass arena (length X width X height: 211 X 144 X 44 mm; see Fig. 1 in Jackson & Pollard, 1990) and left together until they interacted three times or one spider killed the other. The spider that retreated in at least two interactions, or the spider that was killed, was the 'loser' and the other was the

'winner'.

A petri dish was used for a test chamber (Fig. 1). A piece of blotting paper, over which one donor had walked, was cut in half. One half was taped to the base of the petri dish (Fig. 1B) and the other half was taped directly to the top of the petri dish above the lower piece (Fig. 1A). Blotting paper from the other donor was taped to the top and bottom of the other half of the petri dish. The side on which each donor's draglines were placed was determined at random for each test.

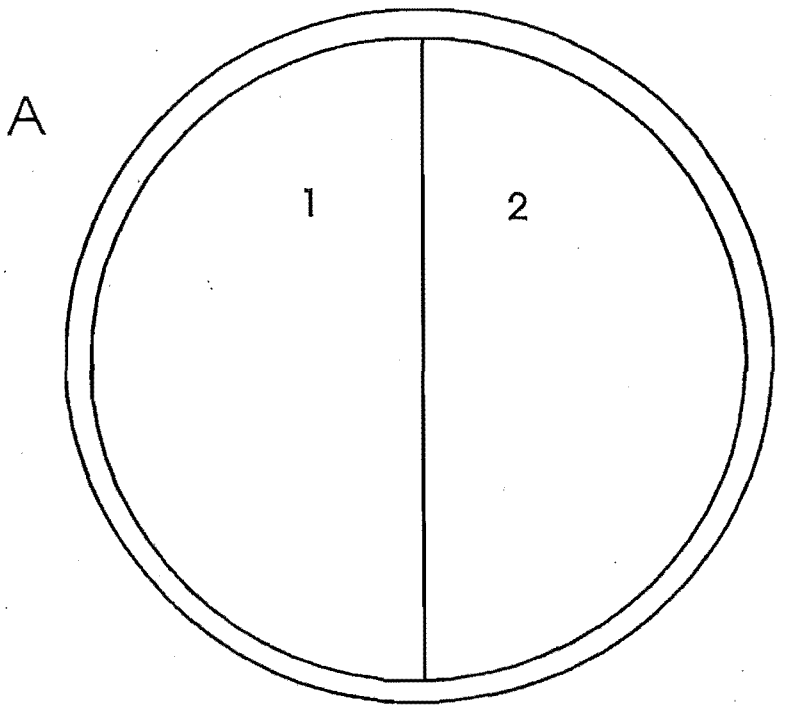
A triangular space (each side 15 mm long), called the 'neutral area', was cut out of the blotting paper on the bottom of one end of the test chamber (Fig. 1). The neutral area straddled the blotting paper from the two donor spiders.

A horseshoe-shaped metal barrier was positioned around the neutral area. Previous studies (Clark & Jackson, 1994a) have shown that, in the absence of this barrier, *P. labiata* is less inclined to react to draglines, possibly because it can see that no other *Portia* is present in the petri dish.

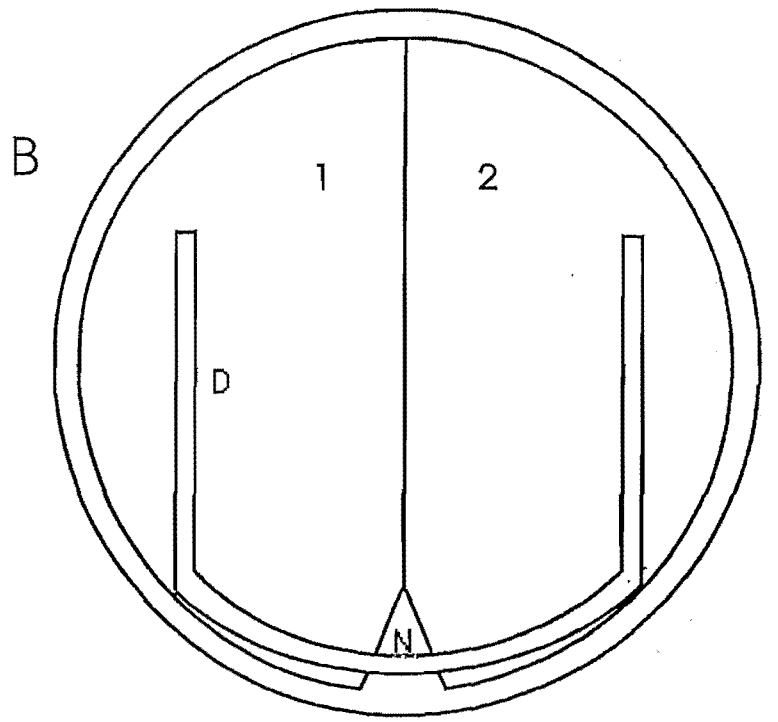
Tests began 10 min after the donor spiders had fought (max. of 1 h after dragline collection) by placing the test spider in the neutral area of the test chamber. Once the test spider walked onto the blotting paper, we recorded over the next 10 min the time spent walking on the blotting paper from each of the two donor spiders. Time in seconds spent walking on the winner's draglines was subtracted from time spent walking on the loser's draglines. Data were analysed using two-tailed Wilcoxon signed-rank tests for paired data (Sokal and Rohlf, 1995).

Fig. 1 Test chamber made from petri dish (diameter 90 mm) for dragline-discrimination tests. A: Top of dish. B: Bottom of dish. 1. Blotting paper covered by draglines of one donor spider. 2. Blotting paper covered by draglines of different donor spider. N: Neutral area (no draglines) onto which test spider is introduced at start of test. d: Metal divider that prevents test spider from seeing entire test chamber at start of test.

Top of petri dish



Bottom of petri dish



Mirror-image tests

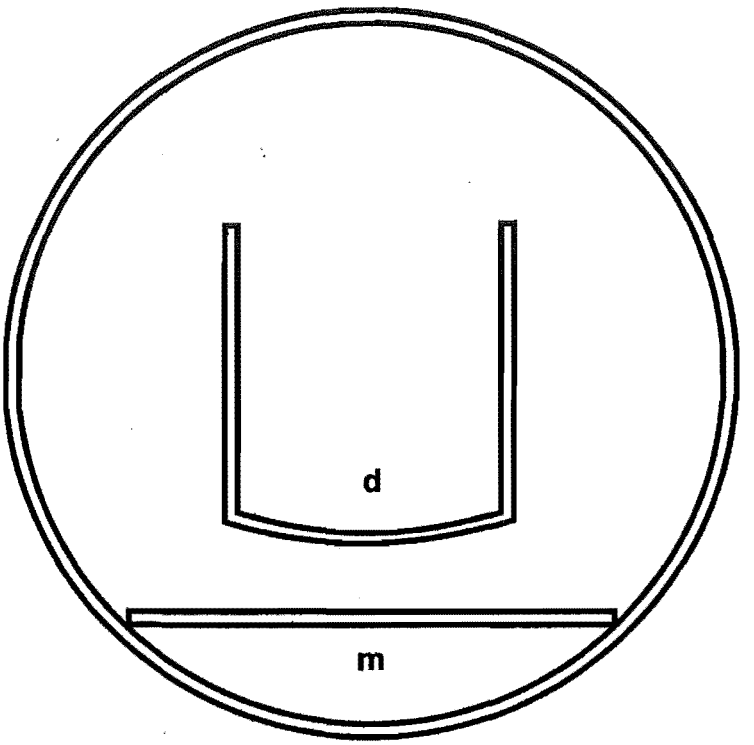
Methods were as in the dragline-discrimination tests except where noted otherwise. Larger petri dishes were used (148 mm in diameter). There was a mirror (length 85 mm; Fig. 2) at the end of the petri dish opposite the neutral area, and the horseshoe-shaped barrier was positioned between the mirror and the neutral area. The mirror was the same height (15 mm) as the dish. Each spider was tested one day with draglines of one donor and the next day with draglines from the other donor (order random). Interactions between the donors were not staged until 10 min after the second day of dragline testing. Draglines of donor 1 and 2 were collected 30 min before the test on the first and second day, respectively. Tests lasted 10 min, during which time the test spider's location (whether or not it was behind the barrier) and display behaviour were observed. Displays were species-specific postures and patterns, leg and palp movements that normally occur in female-female interactions (Jackson & Hallas 1986a). Two-tailed Wilcoxon signed-rank tests for paired data were used to analyse the results.

Two types of display are characteristic of intraspecific interactions in *Portia* (Jackson 1982, Jackson and Hallas, 1986a): 1) postures and movements of the legs, palps and body while the participants are variable distances apart ('non-contact displays'); 2) each spider pressing its forelegs, palps and front of body against the other spider ('embracing'). During tests, the spiders oriented their non-contact displays to the mirror, and they embraced by pressing against the mirror.

Frequency of injury and death

Data from earlier testing (Jackson, 1982; Jackson and Hallas, 1986) were pooled with data

Fig. 2 Test chamber made from petri dish (diameter 148 mm) for mirror-image tests. m: Mirror which provides virtual rival with which test spider interacts. d: Metal divider which provides space in which mirror is out of test spider's view.


d
m

from additional tests of the same kind done in the current study. In these tests, two size-matched females (within 1 mm in body length) were placed in cages together. Cages were comparable in size to the glass arenas used in the mirror-image tests (see above). The pair of spiders was allowed to interact only once, and no two spiders were paired together more than once. Species comparisons of the frequency with which injury (definition: an animal bled or lost an appendage during the interaction) and death occurred during staged interactions between conspecific females were made using 2 X 2 tests of independence with Bonferroni adjustment (Sokal and Rohlf, 1995).

RESULTS

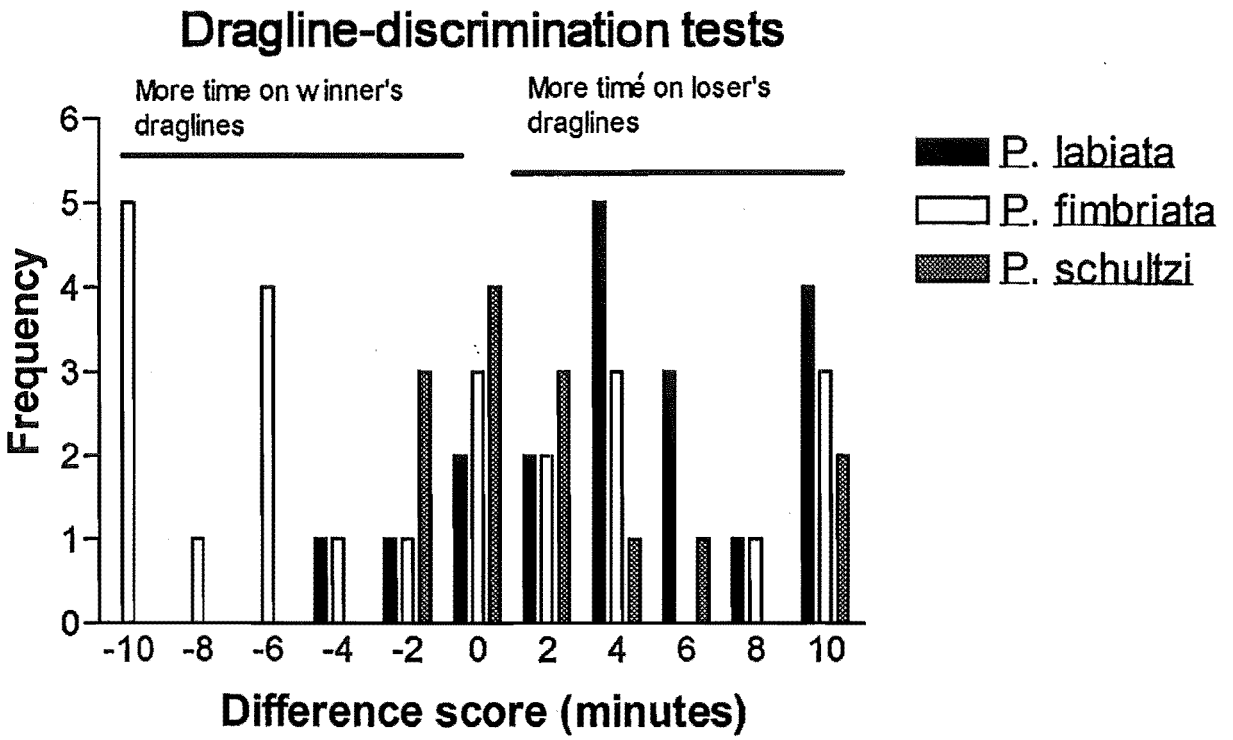
Dragline-discrimination tests

P. labiata females tended to spend more time on the side of the test chamber covered by draglines from the loser (donor spider that lost the contest) instead of the winner (Fig 3; Wilcoxon test comparing time on loser's draglines minus time on winner's, $N = 19$, $P<0.01$). For *P. fimbriata* ($N = 23$, $P = 0.140$) and *P. schultzi* ($N = 14$, $P = 0.475$), there was no statistical evidence that the amount of time was spent on the loser's and winner's draglines differed (Fig. 3). For *P. schultzi* females, data were clustered close to a score of zero (equal time on the two donors' draglines), although there were two individuals that spent all of their time on the loser's draglines. Data from *P. fimbriata* females were spread more evenly across the range of possible scores.

Mirror image tests

The source of the draglines influenced both the time spent embracing and the region of the test chamber favoured by the spider when on the winner's draglines. *P. labiata* females

Fig. 3 Responses of *Portia* females in dragline-discrimination tests. Test spider observed for 10 min in test chamber (Fig. 1) covered by draglines of two donor spiders that had fought each other. No. of test spiders: *P. labiata* (19), *P. schultzi* (17), *P. fimbriata* (23). Each test spider provided a difference score (time in minutes spent on loser's draglines minus time on winner's draglines). Frequency is number of test spiders plotted against difference scores. Scores of *P. labiata* tended to be greater than zero (Wilcoxon signed rank test, $P<0.01$). Scores for *P. schultzi* and *P. fimbriata* not significantly different from zero (Wilcoxon signed rank test, N.S.).


Dragline-discrimination tests
More time on winner's draglines
More time on loser's draglines
Frequency
0
1
2
3
4
5
6
-10
-8
-6
-4
-2
0
2
4
6
8
10
Difference score (minutes)
P. labiata
P. fimbriata
P. schultzi

spent less time embracing (N = 11, P<0.05) (Fig. 4) and more time hidden (N = 11, P<0.05) (Fig. 5) than when on the loser's draglines. There were no differences for *P. fimbriata* (N = 10; embracing, P = 0.262; hidden, P = 0.407) or *P. schultzi* (N = 11; embracing, P = 0.894; hidden, P = 0.505) (Figs 4 and 5).

Frequency of injury and death

Injury and death were more often the outcome in interactions between *P. labiata*: (Table 1) compared with *P. fimbriata* (fatalities: X^2=84.07, P<0.001; injuries: X^2=117.16, P<0.001); compared with *P. schultzi* (fatalities: X^2=13.5, P<0.001; injuries: X^2=26.4, P<0.001).

DISCUSSION

By staging contests, we established an individual within each pair as the winner of the contest and interpreted this as evidence that this individual had superior fighting ability and was more dangerous. *P. labiata* females, when given a choice, tended to spend less time on the draglines of the conspecific female with superior fighting ability and more time on the draglines of the conspecific female with inferior fighting ability. Also, when a virtual rival (i.e., mirror image) could be seen, *P. labiata* appeared to minimise risk by spending less time embracing and more time hidden if the draglines came from a conspecific female with greater, rather than lesser, fighting ability. In both types of testing, *P. labiata* appeared to behave in a manner consistent with greater caution in the presence of signpost cues from a more dangerous rival. Draglines of *P. labiata* females appeared to reveal information about their fighting ability. There was no statistical evidence for this in *P. fimbriata* or *P. schultzi*.

Our data indicate that the frequency of death and injury in female-female interactions, although high for all three species of *Portia*, was especially high for *P. labiata*. Our data came

Table I. Number (proportion) of staged contests that ended with fatality or injury (lost leg or bled) of one or both of the contestants.

Species	No of contests staged	No of contests during which there were fatalities	No of contests during which there were injuries
Portia labiata	610	202 (0.33)	179 (0.29)
Portia fimbriata	656	77 (0.12)	41 (0.06)
Portia schultzi	569	133 (0.23)	95 (0.17)

Fig. 4 Responses (time in minutes spent embracing: see text) of *Portia* females in mirror-image tests. Test spider observed for 10 min in test chamber (Fig. 2) covered by draglines of one of two donor spiders that had fought each other. Tests on alternate days (draglines of the winner on one day, and the loser on the other day; order random). No. of test spiders: *P. labiata* (10), *P. schultzi* (11), *P. fimbriata* (11). Each test spider provided a difference score (time spent embracing when on loser's draglines minus time spent embracing when on winner's draglines). Frequency is number of test spiders plotted against difference scores. Scores for *P. labiata* tended to be greater than zero (Wilcoxon signed rank test, $P<0.05$). Scores for *P. schultzi* and *P. fimbriata* not significantly different from zero (Wilcoxon signed rank test, N.S.).

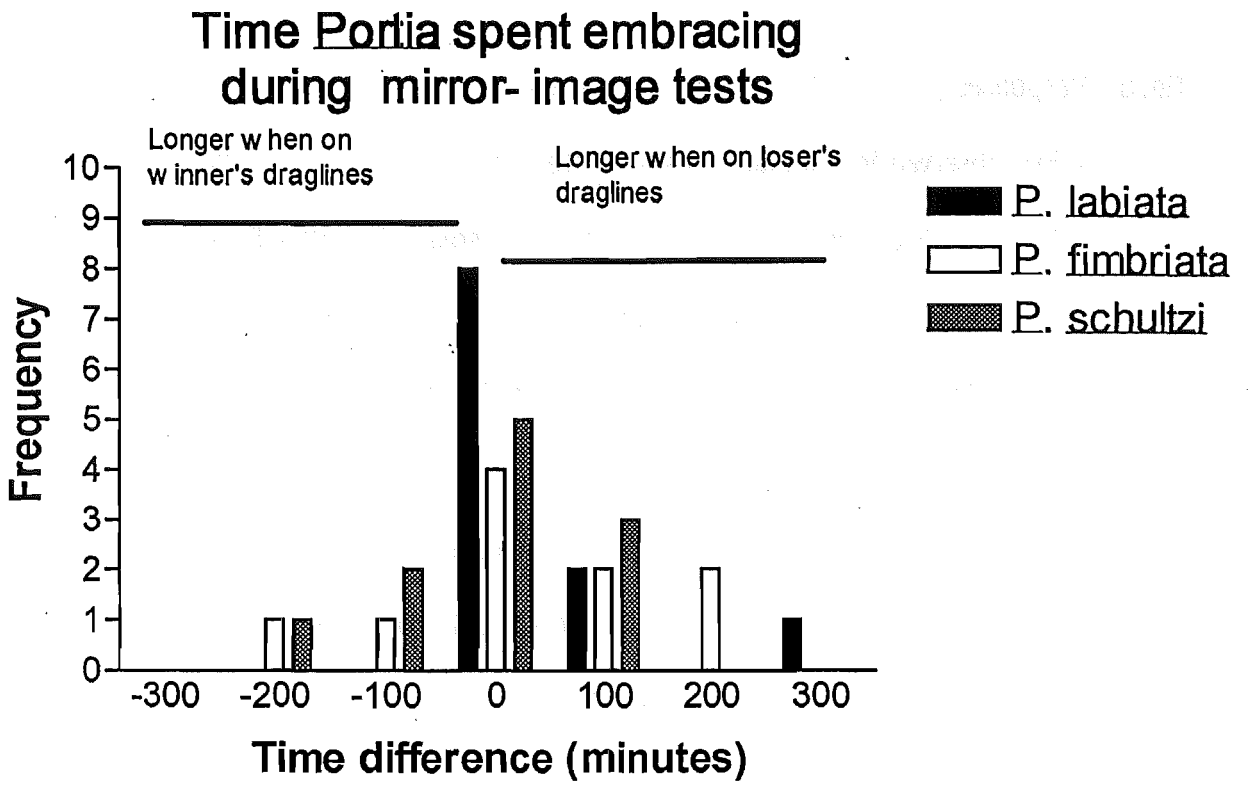
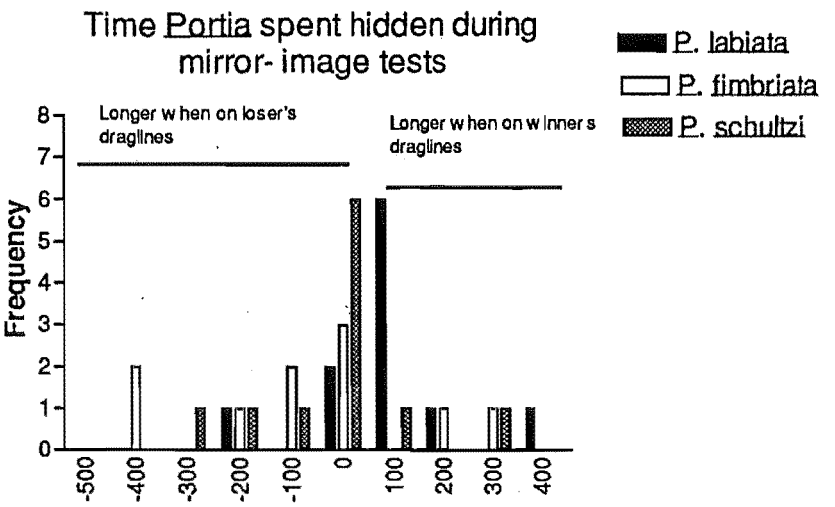

Time Portia spent embracing during mirror- image tests
Longer w hen on w inner's draglines
Longer w hen on loser's draglines
P. labiata
P. fimbriata
P. schultzi
Frequency
10
9
8
7
6
5
4
3
2
1
0
-300
-200
-100
0
100
200
300
Time difference (minutes)

Fig. 5 Responses (time in minutes spent hidden: see text) of *Portia* females in mirror-image tests. Test spider observed for 10 min in test chamber (Fig. 2) covered by draglines of one of two donor spiders that had fought each other. Tests on alternate days (draglines from the winner on one day and the loser the next day; order random). No. of test spiders: *P. labiata* (10), *P. schultzi* (11), *P. fimbriata* (11). Each test spider provided a difference score (time spent hidden when on the winner's draglines minus time spent hidden on loser's draglines). Frequency is number of test spiders plotted against difference scores. Scores for *P. labiata* tended to be greater than zero (Wilcoxon signed rank test, $P<0.05$). Scores for *P. schultzi* and *P. fimbriata* not significantly different from zero (Wilcoxon signed rank test, N.S.).


Time Portia spent hidden during mirror- image tests
P. labiata
P. fimbriata
P. schultzi
Longer when on loser's draglines
Longer when on winners draglines
Frequency
0
1
2
3
4
5
6
7
8
-500
-400
-300
-200
-100
0
100
200
300
400
Time difference (minutes)

from laboratory studies, and frequencies of death and injury may be considerably different in nature. For example, injury and death may be less common in the field because the spiders can more readily move away from each other. However, it is the ranking of the species by their tendency toward injuring or killing one another that is of primary interest, and there is no obvious reason to suspect that this ranking was affected by laboratory conditions. The failure to find evidence of dragline-mediated detection of fighting ability in the two lower-ranked species suggests that *P. labiata*, the most cannibalistic species, either pays stricter attention to cues that reveal fighting ability or has a greater ability to detect these cues than the other species.

When signals indicating fighting ability are under the control of the sender, cheating might appear easy: if the sender leaves a signpost that exaggerates the sender's ability and motivation to fight, the receiver can not immediately call the bluff of a deceitful sender. However, because it tends to be to the receiver's advantage to ignore easily-faked (i.e., unreliable) signals, these signals would not appear to be evolutionarily stable (Maynard Smith, 1982; Hasson, 1994; Johnstone, 1997). Yet it is difficult to see how the reliability of signposts, such as draglines, is guaranteed.

Perhaps, exaggeration is restricted by 'probing' (see Caldwell, 1986). It might be that in nature *P. labiata* females search out signalling conspecifics and at least sometimes find them and test their fighting ability. However, there is currently no evidence to support this hypothesis from either field or laboratory studies. Another possibility is that the features of draglines that reveal fighting ability can not be easily faked because, for some currently unknown physical reason, the making of these features is a demanding task achievable only by especially fit individuals.

Alternatively it may be that the signposts that reveal fighting ability in *P. labiata* are not

actually signals under the sender's control. Instead, it may be that P. labiata has evolved an acute ability to detect an inadvertently-released dragline-associated cue that leaks information on fighting ability of potential rivals.

Chapter 9:

RELATIONSHIP BETWEEN VIOLENT AGGRESSION IN SALTICIDS AND USE OF PHEROMONES TO OBTAIN INFORMATION ON CONSPECIFICS

INTRODUCTION

Having complex eyes and acute vision (Land, 1969a, b), salticids are cursorial predators that generally make no use of webs (Jackson & Pollard, 1996). Portia, as a striking exception, not only hunts cursorily, but also builds webs that serve as defended territories. From its web Portia makes predatory forays to capture other spiders, its preferred prey (Li & Jackson, 1996a; Li et al., 1997), using web invasion and vibratory aggressive-mimicry signals (Jackson & Blest, 1982a; Jackson & Hallas, 1986a; Jackson, 1992a).

Portia females use their webs as oviposition sites, but rival females sometimes forcefully take over webs, eat the resident's eggs, then use the stolen webs as brooding sites for their own eggs (Jackson & Pollard, 1997). The intensity of territorial conflict varies within the genus, 'violent aggression' (i.e., injurious, and sometimes fatal, fights) being more common in Sri Lankan P. labiata than in Queensland P. fimbriata or Kenyan P. schultzi (Clark et al., in press). A high level of violence during the female-female encounters of Sri Lankan P. labiata may have favoured the evolution of especially pronounced use of dragline-based communication.

Spider communication often relies on cues associated with draglines (Tietjen, 1977; Tietjen & Rovner, 1982; Jackson, 1987), the strands of silk that salticids and many other spiders leave behind as part of normal locomotion (Foelix, 1996). Males of most or all Portia spp. may use dragline-based cues for locating conspecific females (Clark & Jackson, 1995a), but Sri Lankan P. labiata females also distinguish between their own and other conspecifics' draglines (self recognition, Clark & Jackson 1994a), and between draglines of conspecific females of different

fighting ability ('RHP recognition', Clark et al., in press). The present chapter is a step toward clarifying whether other salticids practice self and RHP recognition.

MATERIALS AND METHODS

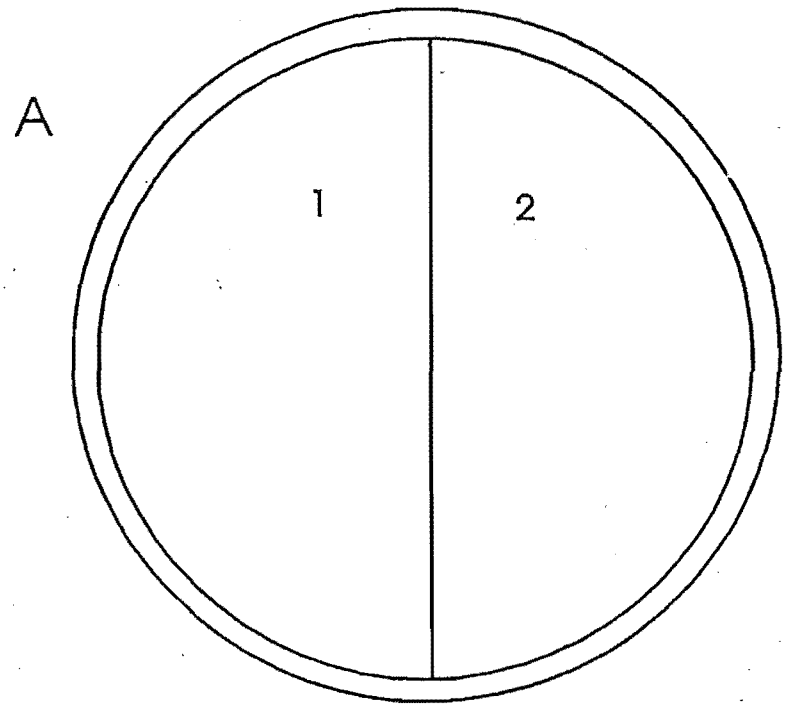
Standard methods for the rearing and maintenance of spiders (Jackson & Hallas, 1986a) and for substrate discrimination tests (Clark & Jackson, 1994a; 1995a, b) were adopted. Only essential details are given here. All salticids tested were adult females of matching size (maximum body length difference: 1 mm). Comparisons are made by using data from previous studies (Clark & Jackson, 1994a; Clark et al., in press) and data from the present study. In total, data considered here come from two populations of P. labiata (one from the Philippines and one from Sri Lanka), another two species of Portia, and seven salticid species from genera other than Portia.

To collect draglines, a salticid (the donor) was placed in a petri dish (diameter 90 mm) in which there was a circular piece of blotting paper taped to the top and bottom, then allowed to walk around for 2 h. The test chamber was another petri dish (Fig. 1). A piece of blotting paper over which a donor had walked was cut in half. One half was taped to the base of the test chamber, the other half being taped to the top directly above the lower piece. Blotting paper from the other donor was taped to the top and bottom of the other half of the test chamber. The side on which dragline-covered blotting paper was placed was determined at random for each test.

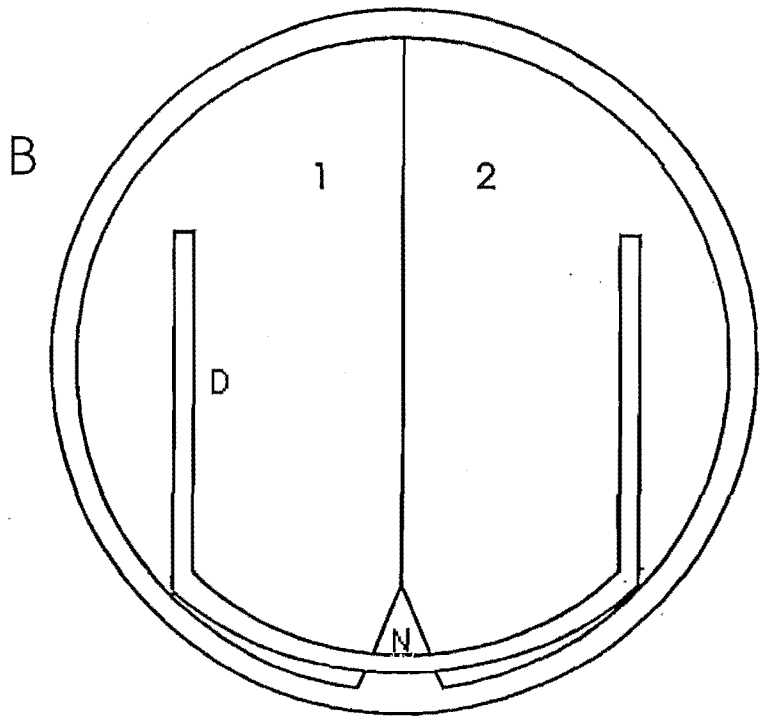
A triangular space (each side 15 mm long), called the `neutral area', was cut out of the blotting paper on the bottom of one side of the test chamber (Fig. 1). The neutral area straddled the blotting paper from the two donor spiders. A test started when a 'test spider' was placed in the neutral area. A horseshoe-shaped metal barrier was positioned around the neutral area because a previous study (Clark & Jackson, 1994a) on P. labiata (Sri Lanka) showed that, in the absence of this barrier, test spiders were less inclined to react to draglines, possibly because it could see that

Fig. 1. Apparatus for dragline-choice tests. Petri dish with two halves of dragline-covered blotting paper on top and bottom of side 1 and two halves of clean blotting paper on top and bottom of side 2. A: top of dish. B: bottom of dish. D: metal divider. N: neutral area.

Top of petri dish



Bottom of petri dish



no other salticid was present.

How long the test spider spent on each type of blotting paper was recorded for 10 min starting as soon as it left the neutral area. Results were analysed using Wilcoxon tests for paired comparisons, applying Bonferroni adjustments for multiple comparisons where appropriate.

FREQUENCY OF INJURY AND DEATH

Methods

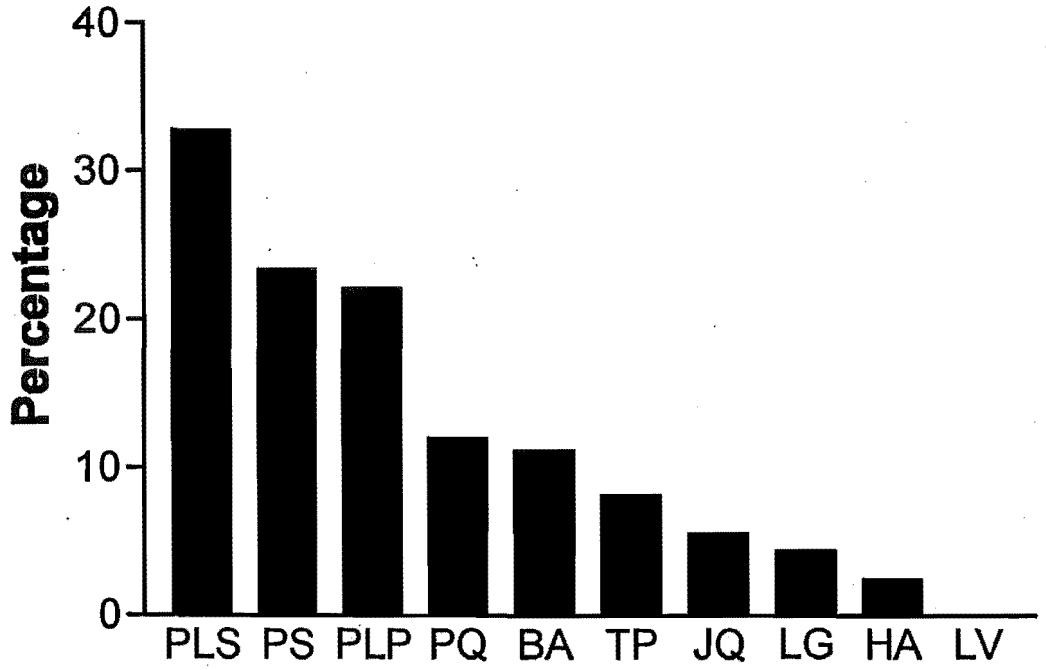
Records were compiled from other studies (Jackson, 1992; R.R. Jackson, unpubl. data) in which interactions between two size-matched conspecific females were staged in cages comparable to the glass arenas used in the present study (see below). Each pair of spiders was allowed to interact only once, and no individual spiders were paired together more than once. The frequency with which injury (definition: an animal bled or lost an appendage during the interaction) and death occurred during staged interactions between females was compared using tests of independence (2 X 2 tables, Sokal & Rohlf, 1995).

Results

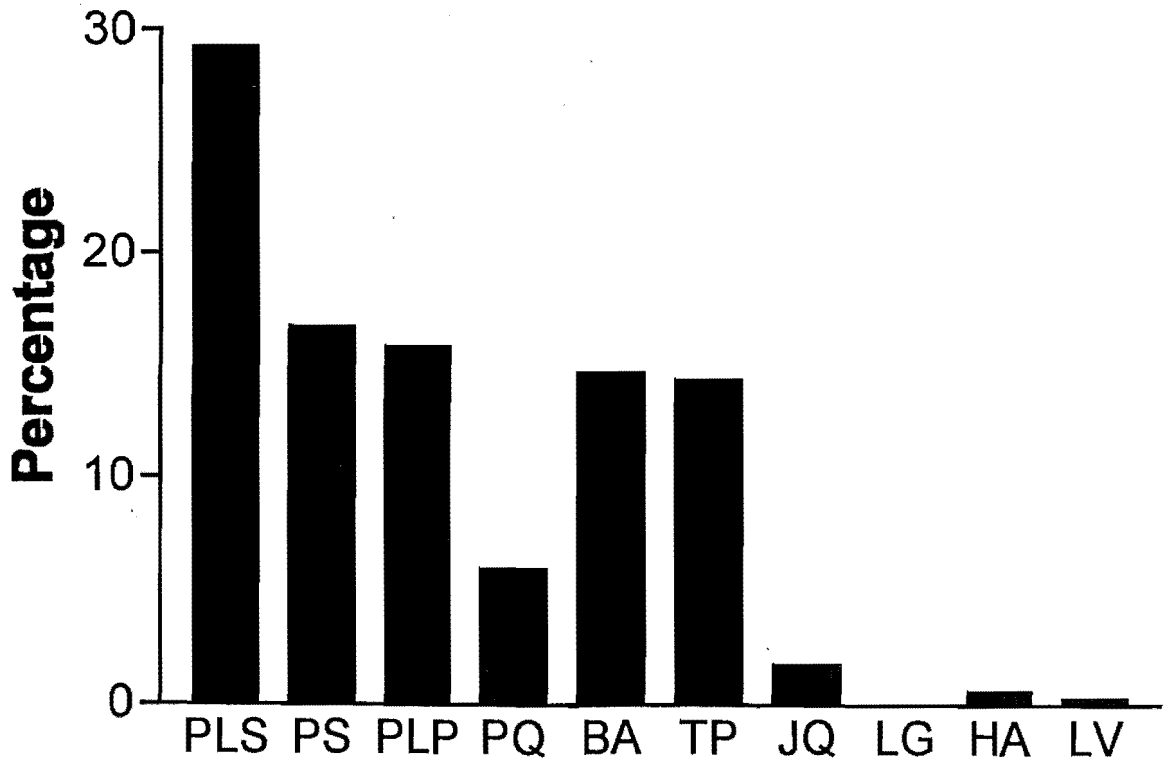
When compared with data from all other species, and when compared with data from Philippines P. labiata, incidences of injuries and fatalities, were greater in Sri Lankan P. labiata (fatalities, Fig. 2A; injuries, Fig. 2B): Philippines P. labiata (fatalities: X^2=8.28, P<0.005; injuries: X^2=13.79, P<0.005), P. fimbriata (fatalities: X^2=84.07, P<0.001; injuries: X^2=117.16, P<0.001), P. schultzi (fatalities: X^2=13.5, P<0.001; injuries: X^2=26.4, P<0.005), Bavia aericeps; fatalities: X^2=80.84, P<0.001; injuries: X^2=39.28, P<0.001), Hasarius adonsoni (fatalities: X^2=111.41, P<0.001; injuries: X^2=109.45, P<0.001), Heratemita alboplagiata (fatalities: X^2=120.64, P<0.001; injuries: X^2=146.89,

Fig. 2. Incidence (percentage of total) of fatalities (A) and injuries (B) during female-female interactions (see text). Abbreviations and sample sizes: Portia fimbriata (Doleschall) from Queensland (PQ; N=656), Portia labiata (Thorell) from Sri Lanka (PLS; N=610); Portia labiata from the Philippines (PLP, N=190); Portia schultzi Karsch from Kenya (PS; N=569); Bavia aericeps Simon from Queensland (BA; N=570); Trite planiceps Simon from New Zealand (TP; N=635); Jacksonoides queenslandicus (Wanless) from Queensland (JQ; 1256); Hasarius adonsoni (Audouin) from Queensland (HA; 317); Heratemita alboplagiata from the Philippines (LG; N=413); Lyssomanes viridus (Walckenaer) from the U.S.A. (LV; N=791).

A. Incidence of fatalities



B. Incidence of injuries



P<0.001), Jacksonoides queenslandicus (fatalities: X^2=250.12, P<0.001; injuries: X^2=325.24, P<0.001), Lyssomanes viridus (fatalities: X^2=306.07, P<0.001; injuries: X^2=259.08, P<0.001) and Trite planiceps (fatalities: X^2=119.03, P<0.001; injuries: X^2=41.29, P<0.01).

RHP RECOGNITION

Methods

For each test, there was a test spider and two donor spiders. The two donor spiders were introduced simultaneously into a glass arena (Fig. 1 in Jackson & Pollard, 1990) and left until they interacted three times or one spider killed the other. The spider that retreated in at least two interactions, or the spider that was killed, was the 'loser'; the other spider was the 'winner'.

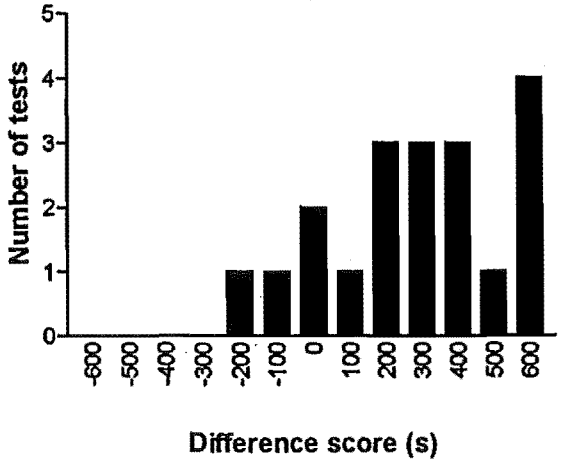
Test chambers were prepared by positioning blotting paper coated with draglines from the contest winner on one side and blotting paper coated with draglines from the contest loser on the other side. Tests began 10 min after the donor spiders had interacted (max. of 1 h after dragline collection).

Results

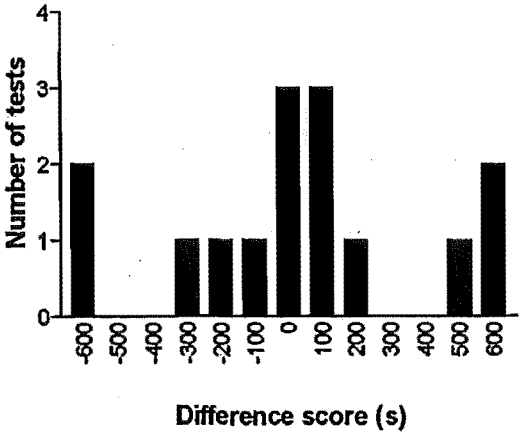
Sri Lankan P. labiata spent more time on the side of the test chamber covered by draglines from the loser instead of the winner (Fig. 3; P<0.01), but there was no statistical evidence from testing Philippines P. labiata or any of the other species that time spent on the loser's and winner's draglines differed. Data from P. fimbriata, P. schultzi, the Philippines P. labiata, Hasarius adonsoni, Euophrys parvula and Heratemita alboplagiata were spread evenly across the range of possible scores. Data from Bavia aericeps, Lyssomanes viridis, and Trite planiceps were centred around zero (i.e., time spent on each type of dragline about equal). Data from J. queenslandicus

Fig. 3. Results of RHP-recognition tests. Spiders given simultaneous access to draglines from the winner of a contest (one side of petri dish) or draglines from the loser (other side of petri dish). All three spiders had no prior experience of each other. Difference score: time spent on winner's draglines minus time spent on loser's draglines. Only in Sri Lankan Portia labiata is there statistical evidence (Wilcoxon signed-rank test for paired comparisons) that test spiders discriminate between contest 'winners' from 'losers' draglines.

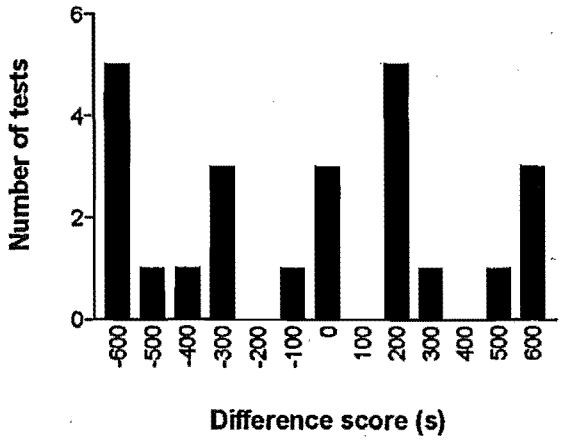
(a) Sri Lanka Portia labiata (N=19)



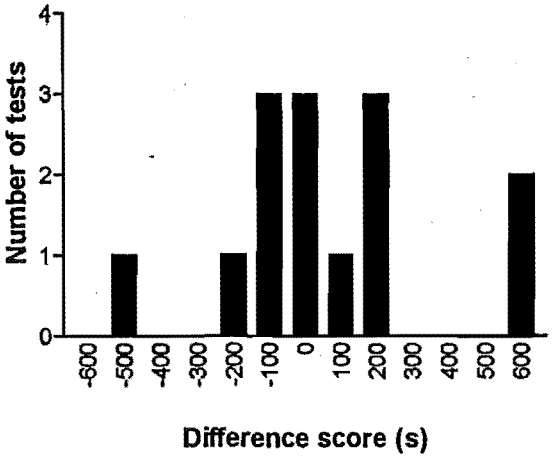
(b) Philippines Portia labiata (N=15)



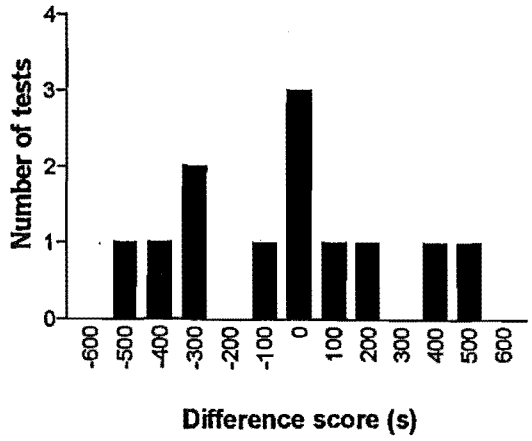
(c) Portia fimbriata (N=24)



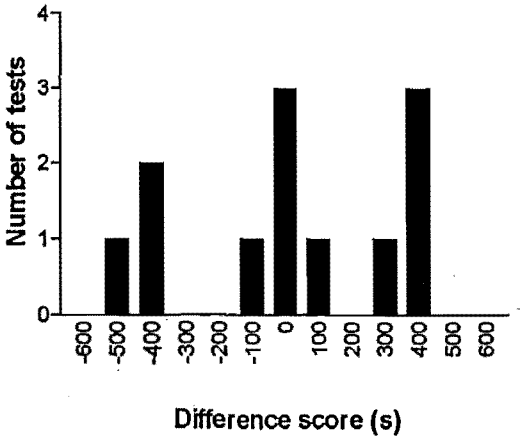
(d) Portia schultzi (N=14)



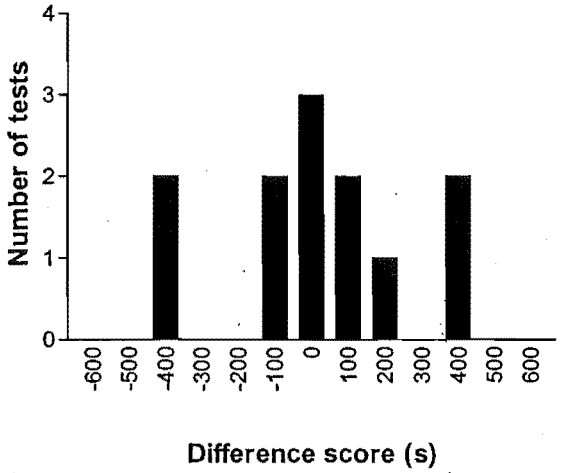
(e) Bavia aericeps (N=12)



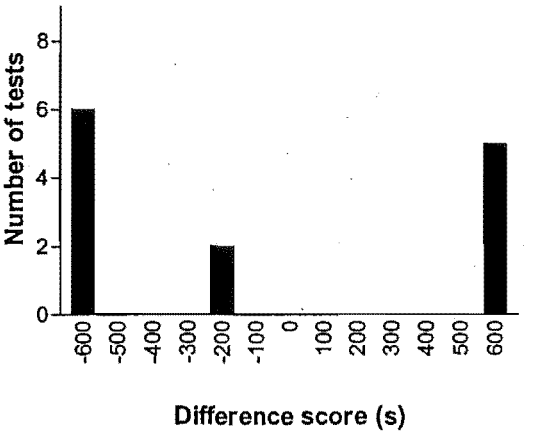
(f) Euophrys parvula (N=12)



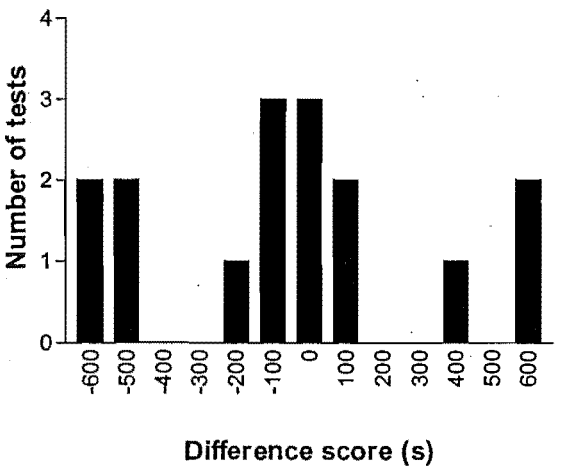
(g) Hasarius adonsoni (N=12)



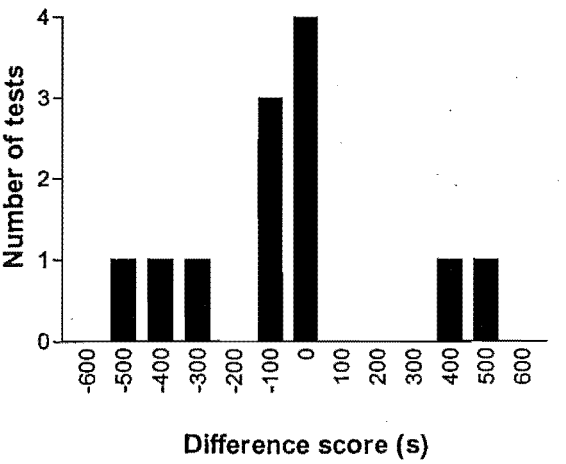
(h) Jacksonoides queenslandicus (N=13)



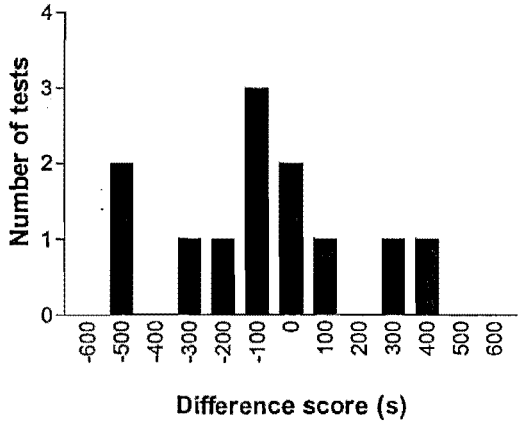
(i) Ligurra sp. (N=16)



(j) Lyssomanes viridus (N=12)



(k) Trite planiceps (N=12)



were bimodally distributed because test spiders tended to spend all their time on the dragline onto which they first stepped.

SELF RECOGNITION

Methods

A test chamber was prepared by placing blotting paper coated with the test spider's own draglines on one side of a petri dish and blotting paper coated with draglines from another conspecific on the other side.

Results

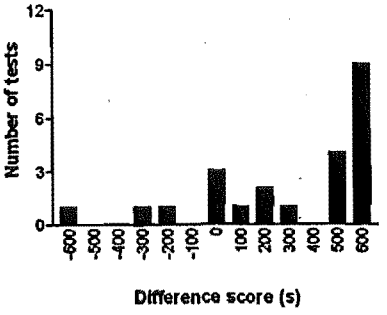
Except for Sri Lankan P. labiata there was no statistical evidence that salticids discriminated between their own draglines and those of other conspecifics (Fig. 4). Results for P. fimbriata and J. queenslandicus were more or less evenly spread over the range of possible values. Results for Philippines P. labiata and Lyssomanes viridis were bimodal. Results for Bavia aericeps, Hasarius adonsoni, Euophrys parvula and Trite planiceps tended to be clustered at zero (equal time on the two types of draglines).

DISCUSSION

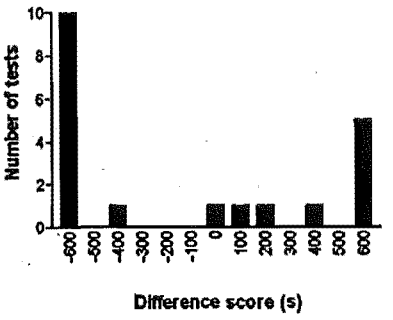
For a salticid subject to high levels of violent aggression, ability to detect self and RHP-revealing cues would appear to be especially advantageous. Distinguishing self-derived draglines from draglines originating from another conspecific might enable a salticid to take precautions when an encounter with a rival is likely. Detecting RHP cues from draglines might enable a salticid not only to prepare for a potential encounter with a rival but also to make pre-emptive adjustments

Fig. 4. Results of self-recognition tests. Spiders given simultaneous access to their own draglines (self) or the draglines of another conspecific (non-self). Data for adult spiders unless stated otherwise. Difference score: time spent on self draglines minus time spent on non-self draglines. Only in Sri Lankan Portia labiata is there statistical evidence (Wilcoxon signed-rank test for paired comparisons) that test spiders discriminate between self and non-self draglines.

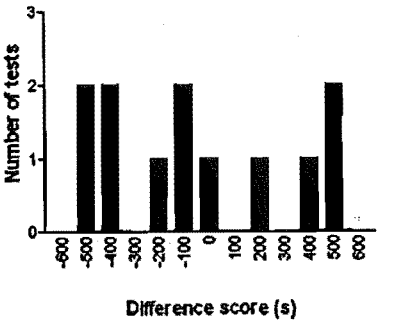
(a) Sri Lanka Portia labiata (N=21)



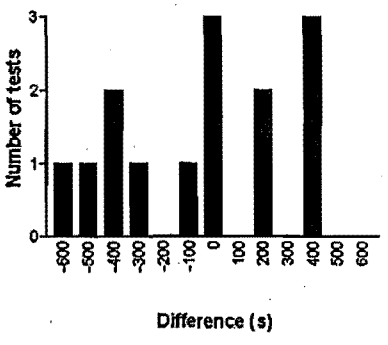
(b) Philippines Portia labiata (N=20)



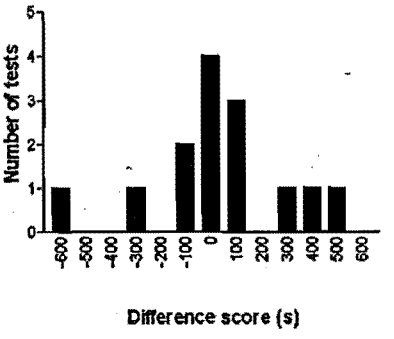
(c) Portia fimbriata (N=12)



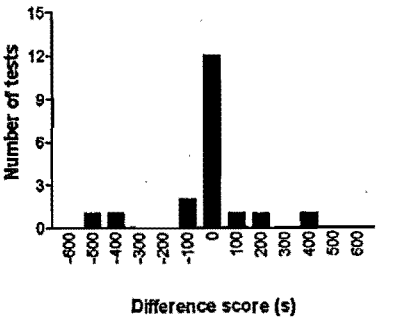
(d) Bavia aericeps (N=16)



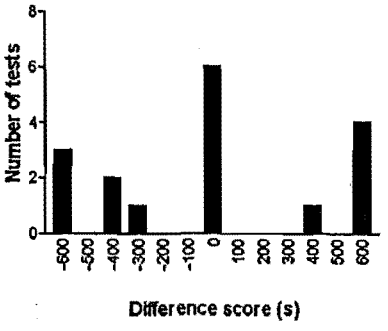
(e) Euophrys parvula (N=14)



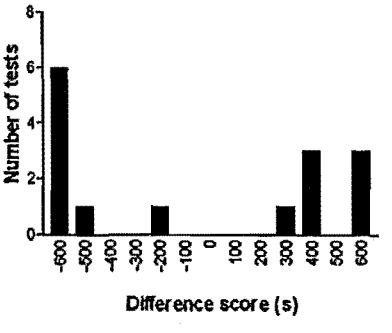
(f) Hasarius adonsoni (N=19)



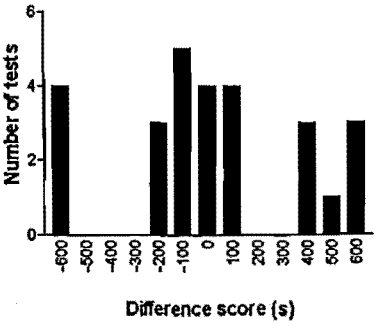
(g) Jacksonoides queenslandicus (N=17)



(h) Lyssomanes viridis (N=13)



(i) Trite planiceps (N=27)



appropriate for how dangerous the rival might be.

Using choice tests (blotting paper) as assays for ability to detect these cues, evidence for self and RHP detection was found for Sri Lankan P. labiata, but there was no statistical evidence found that any other salticid studied detects self and RHP cues on draglines. As the Sri Lankan P. labiata appears to have the highest level of violent aggression, these findings are suggestive of a relationship between the incidence of violent aggression in salticids and the salticid's reliance on chemical cues from potential rivals.

Additional testing is needed not only on a wider range of salticid species, but also on males. In some salticids, violent aggression is more prevalent in males than in females, and therefore it might be predicted that in some species males rely more strongly than females on RHP and self-recognition cues. With all salticids studied, but especially with Sri Lankan P. labiata, details would be useful on how information derived from self and RHP cues on draglines might be used in nature, or in more natural environments in the laboratory.

Even with these limitations, the Sri Lankan P. labiata appears to be an unusual salticid. Why especially violent aggression might have evolved in this particular salticid is unclear. In general, research on the intraspecific interactions of this salticid in nature is needed.

CHAPTER 10: DISCUSSION

1. Adaptive trade-offs: the larger question that formed the context of the thesis research

At some level, the idea that adaptive trade-offs constrain the evolution of complex mental activity in animals, including humans, seems incontestable. An animal's brain has a finite number of neurones and connections. There must be limits on how much information can be processed and how fast it can be processed. Additionally, there must be limits on the complexity of the behaviour controlled by the brain. Trade-offs seem inevitable if an animal is operating close to those limits. Becoming better at one mental activity would seem to be detrimental to how well other mental activities are carried out. Implicitly, it is especially animals with small brains that we might expect to be more severely constrained by such trade-offs.

Psychological studies of both human and non-human animals show limitations in ability to process information related to multiple problems simultaneously (Dukas & Real, 1993), implying a trade-off in attention: an animal attends to one task, increasing the efficiency with which it can be performed, but at a cost, at least in the short term, to the performance of other tasks.

Accepting that animals assimilate only a limited proportion of the information received from the environment suggests there are clear advantages to abilities to focus attention on stimuli relevant to the activity being carried out (Dukas, 1998). Arthropod brains being small are generally envisaged as vastly less complicated than vertebrate brains, suggesting that arthropods are more severely constrained in their ability to assimilate information from the environment. That trade-offs set greater restrictions on arthropods than vertebrates in the proliferation of mental ability and behavioural complexity must be true at some level, but

precisely how severe restrictions imposed by trade-offs are is not clear. How large is the gap between arthropods and vertebrates?

Using salticid spiders as a case study, I investigated the severity of adaptive trade-offs. Salticids were chosen because they are unique spiders with a highly evolved visual system and intricate vision-based prey-capture behaviour. If trade-offs are especially important in arthropods, then we might expect the evolution of the salticid's complex eyes, acute vision and efficient vision-based predatory behaviour to have been achieved at a cost to sensory and predatory systems based on other modalities.

An extreme trade-off would have been implied if salticids had been found to make little or no use of sensory modalities other than vision. However, earlier studies have shown that salticids make extensive use of sensory modalities other than vision to mediate courtship and other types of intraspecific communication (Jackson & Pollard, 1997), with no evident cost or trade-off. For example, non-salticid spiders tend to have rudimentary eyesight and rely instead on other modalities such as chemoreception (sex pheromones) during courtship. Yet there is no evidence that salticids are less efficient than non-salticid spiders at using sex pheromones. The present study suggests that a parallel conclusion applies to predatory behaviour.

I focused on two species of salticid, one of which was araneophagic (Portia fimbriata (Doleschall)) and the other myrmecophagic (Habrocestum pulex (Hentz)). Being salticids, both have highly developed visual systems, yet both species apparently make extensive use of chemical information in the context of predation. It seems that the significance of sensory trade-offs is far from obvious, not only for intraspecific communication but also for predatory strategies in salticids.

2. **Specificity of chemical cues**

For both species studied, prey identification by chemical cues was implicated by: (1) choice tests using contact chemical cues (substrate-choice tests) and olfactory cues (olfactometer tests); (2) postural and behavioural changes in response to contact chemical cues; and (3) effects of chemical cues on attention to lures.

H. pulex was shown to have the ability to identify ants using chemical cues alone. Experiments with commercially available 6-methyl-5-hepten-2-one (an ant alarm pheromone; Hölldobler & Wilson, 1990; Blum 1992) and with live ants that are not natural prey suggest that H. pulex distinguishes ants from other prey, rather than identifying particular ant species. H. pulex's sensory system appears to include a generalised ant detector.

In contrast, experiments using P. fimbriata imply a greater level of specificity. Although typical salticids from other genera tend to be primarily insectivores, P. fimbriata is araneophagic. Typical insectivorous salticids are one of several broad categories of spiders taken by Queensland P. fimbriata. Many web-building spiders from other families are also preyed on. However, P. fimbriata responded specifically to the chemical cues from Jacksonoides queenslandicus Wanless. This species is the most abundant salticid in the Queensland rainforest habitat of P. fimbriata, and the present study suggests that a tight relationship has evolved between the predatory strategy and sensory system of P. fimbriata and this particular prey species.

3. Factors favouring the use of chemical cues for prey identification by araneophagic and myrmecophagic salticids

For salticids, ants and spiders are unusual prey. The risk that an ant or spider prey might injure or kill the potential predator may be exceptionally high for araneophagic and myrmecophagic salticids. Furthermore, high risk of injury or death may exert a strong selective pressure favouring predators that gain an early warning of a dangerous prey's presence. If warned, a predator can potentially prepare for a predatory encounter and reduce the risk of being attacked and injured. Chemical signals may be especially effective as early detection cues. Although most salticids have acute vision and can potentially identify prey from a distance, this requires an unobstructed line of sight. For H. pulex living in leaf litter, and P. fimbriata hunting in a complex rainforest environment, reliance solely on seeing an ant or spider from a distance may be excessively risky. Chemical cues are effective despite obstructions to a predator's line of sight. Chemical cues can provide a predator with information about what prey are in the vicinity, how far away they are (olfactory cues: Bossert & Wilson, 1963), and the time since the cue was deposited (signpost cues: Alberts, 1992). In contrast, optical cues are especially good at revealing the exact location of both predator and prey.

For Queensland P. fimbriata, relying solely on optical cues to detect salticid prey may be especially problematic, as all salticids have acute vision. When the prey is another salticid, the problem for P. fimbriata is that, if the predator can see the prey, then it is also likely that the prey can see the predator. Chemical cues enable P. fimbriata to detect a prey salticid without necessarily being in its field of view. One could logically argue the same problem applies to both optical and chemical cues. If a prey is in range for detection of chemical cues

by the predator, then the predator may also be in range for detection of its chemical cues by the prey. However, this is a problem only if the predator and prey are both sensitive to chemical cues from each other, and are able to determine each other's location from these cues. For P. fimbriata and J. queenslandicus, detection of chemical cues seems to be one sided.

I tested J. queenslandicus for the ability to detect chemical cues from P. fimbriata, and no evidence of this was found. This may not be surprising, as the population of J. queenslandicus in Queensland rainforests is very large. As a prey animal J. queenslandicus may be very significant for P. fimbriata, whereas P. fimbriata is probably only one of many predators of J. queenslandicus. This may account for why the chemosensory system of P. fimbriata appears to have become tuned to chemical cues coming from J. queenslandicus but not vice versa. With ants and H. pulex, sensitivity to chemical cues may also be one sided. Although the ability of ants to detect H. pulex was not tested, it is unlikely that H. pulex has a major impact on ant populations, and it may be unlikely that ants would benefit strongly by being able to detect H. pulex.

There may be important ways in which vision and chemoreception differ. Chemical cues may more often be highly specific. An animal that has a chemosensory system tuned to a specific cue probably can get very precise information about the identity of the animal that left a chemical trace. Tuning may be a factor with reliance on optical cues as well, but perhaps to a lesser extent. For example, even if J. queenslandicus is not tuned specifically to P. firnbriata, optical cues may still be effective because optical cues common to salticids in general, or to some broader category, such as spiders in general, might be sufficient. In contrast, chemical cues do not appear to be as generalised in relation to salticid or spider detection. There was no evidence that P. fimbriata or J. queenslandicus detect chemical cues from spiders or

salticids in general. In contrast, H. pulex appears to have more or less generalised sensitivity to chemical cues from ants.

4. Specialisation by Queensland Portia fimbriata for preying on Jacksonoides queenslandicus

Although Queensland P. fimbriata was tested for sensitivity to chemical cues from a wide range of prey spiders, especially other salticids, it was chemical cues from just one salticid species, J. queenslandicus, that appeared to affect Queensland P. fimbriata's predatory behaviour. There seems to be a parallel sensitivity to optical cues specifically from J. queenslandicus. Chemical cues from J. queenslandicus, but not from any other species tested, evidently trigger an attention shift in Queensland P. fimbriata that facilitates the use of optical cues to find J. queenslandicus. The effect of chemical cues from J. queenslandicus does not appear to make P. fimbriata more responsive to spiders in general, or even salticids in general. Instead, it is the optical cues from J. queenslandicus specifically that Queensland P. fimbriata's attention seems to focus on. Similar links between detection of chemical cues from prey and increased sensitivity to optical cues relating to prey do not appear to have been reported in other predators.

Of course, a trained arachnologist can readily distinguish J. queenslandicus from other spiders. That P. fimbriata with an eye and brain that are minute compared with the human eye and brain can make such fine-grain optical discrimination is remarkable. Small size must surely limit visual perception, but where these limitations lie is unclear. Studies are needed to clarify precisely what optical cues are used by P. fimbriata for making such precise identifications.

Another question of importance is why it is only Queensland P. fimbriata that seems to

single out one particular salticid as so special a prey. Behavioural studies have been carried out on five species of Portia (P. africana, P. albimana, P. fimbriata, P. labiata and P. schultzi) from a wide range of African, Asian and Australian habitats. The Queensland rainforest habitat of P. fimbriata has an exceptionally high density of cursorial salticids, but it is especially J. queenslandicus that accounts for this high density of salticids (Jackson, 1982). Using cryptic stalking, Queensland P. fimbriata is effective at preying on a wide range of salticid species and it is tempting to argue that cryptic stalking evolved as a tactic for capturing salticids in general. An alternative hypothesis is suggested by the present study, that J. queenslandicus, being by far the most abundant salticid in P. fimbriata's Queensland rainforest habitat, may have exerted the primary selective pressure responsible for the evolution of cryptic stalking. The usefulness of cryptic stalking for capturing salticids other than J. queenslandicus may be, to a significant degree, incidental. Not only the highly focused chemosensory system studied here but also cryptic stalking may have been derived by natural selection as an adaptation for capturing this one exceptionally abundant prey species.

5. Attention and prey detection in P. fimbriata

Cryptic prey presents predators with the problem of how to discriminate prey from non-prey. L. Tinbergen (1960) in conjunction with field studies on insectivorous birds proposed that birds learn the characteristics of common prey, and subsequently use search images to locate these prey. However, the emphasis on the role of learning in the literature on search-image use may be misplaced. There would seem to be two parallel issues: how search-images are acquired and how they are used (Plaisted & MacIntosh, 1995). Search-images appear to stimulate the predator to shift its attention to a particular set of characteristics that

identify a particular type of prey. It is this shift in attention which is important in the context of my study.

According to the attention threshold hypothesis (Bond, 1983), predators use neural templates to focus attention on cues from particular prey. The idea is that by attending to one stimulus type at a time, a predator can minimise the mean latency to locate prey. When the frequency with which this stimulus is encountered falls below a certain threshold level. My results have been consistent with this model. Firstly, when in cages with draglines from J. queenslandicus, the latency to find J. queenslandicus lures is less than other species. This is evidence that P. fimbriata is attending to the specific optical cues that identify J. queenslandicus. Secondly, when optical cues from J. queenslandicus are not encountered, P. fimbriata seems to switch to a more generalised attentional state. The evidence for this is how P. fimbriata becomes more likely with the passage of time to accept other lures as prey. That is, after searching for some time, P. fimbriata's attention appears to become less focused, and lures with characteristics that only crudely correspond to J. queenslandicus seem to become effective at triggering P. fimbriata's cryptic stalking behaviour.

6. **Conclusion**

Theoretically, the small size (cf. vertebrates) of the arthropod nervous system should constrain the use of multiple sensory modalities by arthropods. I assessed this hypothesis using two salticid spiders, P. fimbriata and H. pulex. Although salticids have a highly evolved visual system, I have shown that chemical cues are of similar importance to optical cues for detecting prey animals. This suggests that adaptive trade-offs in sensory biology may not have affected the adoption of multiple sensory modalities in salticids.

Secondly, the ability of these species to use sensory modalities concurrently was assessed. Experiments using lures showed that both P. fimbriata and H. pulex, upon encountering chemical cues from their preferred prey, increase their attention to optical cues corresponding to those prey. Integration of sensory modalities in this way does not seem to have been demonstrated in other predators.

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